THE ECOLOGY OF WOODLAND CARIBOU IN CENTRAL SASKATCHEWAN

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ABSTRACT

Habitat selection has been described as a hierarchical process that may yield various patterns depending on the spatial and temporal scales of investigation. I employed forest cover data and animal locations obtained through satellite radio-telemetry to examine patterns of habitat selection by female woodland caribou (*Rangifer tarandus caribou*) in central Saskatchewan. I began with random sampling of various types of forest stands focused on vegetation strata shown elsewhere to be of importance to woodland caribou. Cluster analysis and ordination by nonmetric multidimensional scaling suggested that six vegetation community types be recognized. Canonical correspondence analysis revealed strong relationships between the vegetation communities and data on canopy characteristics contained in the provincial forest inventory.

Woodland caribou in Saskatchewan are now aggregated into several spatially disjunct populations. With regard to reproduction, first conception by females occurred at 16 months; the overall pregnancy rate was 94%; and the minimum parturition rate was 86%, all of which indicate adequate nutrition. The annual survival rate of adults was 84%, which is comparatively low. Calf recruitment was also low (28 calves:100 cows), which I suspect was due to predation.

Wolves (*Canis lupus*) have long been thought to limit woodland caribou populations while subsisting on moose (*Alces alces*), but I speculate that black bear (*Ursus americanus*) predation may be an important cause of poor calf survival.

My habitat selection work was conducted at both coarse (seasonal range) and finer (daily area) scales. Female caribou selected peatlands and black spruce dominated stands over recently disturbed stands and early seral stage forests in all five populations studied. This pattern may reveal the effective avoidance of wolves, the primary factor limiting caribou throughout the boreal forest. In three populations where coarse level selection suggested a relative preference of young forest stands or clearcuts, I found a reversal in selection patterns at finer scales. I interpret this to indicate that remaining populations are relics of a once more continuous distribution, and that their coarse level selection best describes historic rather than current selection. I determined that the hierarchy of habitat selection reflected the hierarchy of factors actually or potentially limiting caribou populations.

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1. General Introduction

1.1 Habitat selection

The study of selective behaviour by animals can answer fundamental questions in ecology, as it reveals the priorities of individuals in acquiring the resources by which they meet their needs for survival and reproduction. Johnson (1980) described habitat selection as an inherently hierarchical process in which selection is specific to some scale of space and time. At the coarsest scale, habitat selection is equated with the range over which a species is distributed. At progressively finer scales it proceeds to describe the ranges occupied by populations, the ranges occupied by individuals, on through to the ephemeral decisions like where next to move, to forage, or to rest.

The pattern of selective behaviour may persist over a range of spatial and temporal scales but vary among ranges of scales (Wiens 1989; With and Crist 1995). Depending on the scale observed, the biological processes responsible for the selective patterns may differ (Poizat and Pont 1996). The choice of observational scales is therefore critical, and should be defined by ecological criteria rather than human constraints (Poizat and Pont 1996).

Wallace *et al.* (1995) stressed the importance of defining these criteria, after first identifying the relationships between environmental heterogeneity and the functions of organisms. Turner *et al.* (1995) further emphasized that the scale of study should relate to the processes of interest.

As with any biological question, we should expect the relationship between organism and environment to be revealed by revisiting the underlying theory that unifies the discipline - evolution by natural selection. The processes of interest that Turner *et al.* (1995) refer to should be the factors that potentially limit individual fitness. A knowledge of factors that have the potential to limit a population can direct the scale of investigation to determine the environmental features that affect individual ability to overcome those limiting factors. Habitat patterns should affect animal behaviour by presenting an individual with the resources by which it can best avoid the factors that stand to limit its lifetime reproductive success. Because lifetime reproductive success hinges on a series of choices, we should expect to find the behaviour of individuals, and by extension, the populations and species to which they belong, to be anything but random.

1.2 Habitat selection studies

Habitat selection studies typically operate by comparing some measures of habitat use with parallel measures of habitat deemed available. A great deal of effort and journal space has recently been devoted to the debate on how to determine habitat availability (*e.g.*, Johnson 1980; Thomas and Taylor 1990; Arthur *et al.* 1996) and on how to statistically analyze data to determine if selection is occurring (*e.g.*, Alldredge and Ratti 1986; Alldredge and Ratti 1992; Manly *et al.* 1993; Aebischer *et al.* 1993; Arthur *et al.* 1996). Locations of individual animals are typically given equal weight in estimating the relative amount of use that an animal makes of each habitat category (Porter and Church 1987; White and Garrott 1990).

The habitat mosaic, the arrangement of various habitat types, is critical to how individuals perceive and select habitat for their use (Wiens 1989; With and Crist 1995; Turner *et al.* 1995). Occupancy of a given habitat patch may depend on characteristics of adjacent patches (Turner *et al.* 1995) including the densities of their animal populations (Wiens 1989). Despite the likely importance of the characteristics of adjacent habitat types, selection studies relying on radio-telemetry data have traditionally attempted to restrict habitat use at each location to a single habitat type (*e.g.*, Nams 1989; White and Garrott 1990; Samuel and Kenow 1992; North and

Reynolds 1996; but see *e.g.*, Gawlik and Bildstein 1993; Ripple *et al.* 1997). An additional problem is that radio-telemetry bias may result in animals going undetected in some habitat types (North and Reynolds 1996).

The determination of habitat selection is inadequate without an understanding of the cause and effect relationships between habitat selection and the demographic performance of the animal population (Hobbs and Hanley 1990). Decisions regarding land use require knowledge not only of habitat selection patterns, but of the effects of those patterns on the population (Hobbs and Hanley 1990).

An issue that is not well addressed in the literature is the importance of defining habitat categories by variables that relate to factors which may be limiting to the population being studied. Without carefully delineated habitat categories the results of selection studies may be difficult to interpret.

1.3 Historical perspective

Woodland caribou (*Rangifer tarandus caribou*) in Saskatchewan range from the southern limits of the ranges occupied by the Beverly and Qamanirjuaq herds of barren-ground caribou (*R. t. groenlandicus*), to the southern margin of the boreal forest. Early reports suggested that there were few interactions among individual groups of caribou in the region (Ruttan 1960), suggestive of several

populations within a metapopulation (*sensu* Wells & Richmond 1995).

Rock (1992) concluded that most human impacts on caribou habitat in Saskatchewan have been restricted to the area south of the Churchill River, particularly in the area south of the Precambrian shield that contains the province's commercial forestry operations. This is the region in which my research was conducted (Fig. 1.1). In 1966 the province's first pulp mill was constructed, and road building began in the southern boreal forest. Local reports indicated that increased hunting followed the increase in logging activity and road construction, and resulted in the decline or disappearance of many local caribou populations (Trottier 1988). A similar pattern of decline or extirpation of woodland caribou populations following human activity has occurred across North America (Bergerud 1974). In central Saskatchewan, minimal levels of subsistence hunting (Trottier 1986) and the end of sport hunting in 1986 should have produced an increase in the caribou population in the absence of major limiting effects of food shortage, disease, or predation.

1.4 Objectives

Overall, my objective was to characterize and explain patterns of habitat selection by woodland caribou in central Saskatchewan. This work begins with the

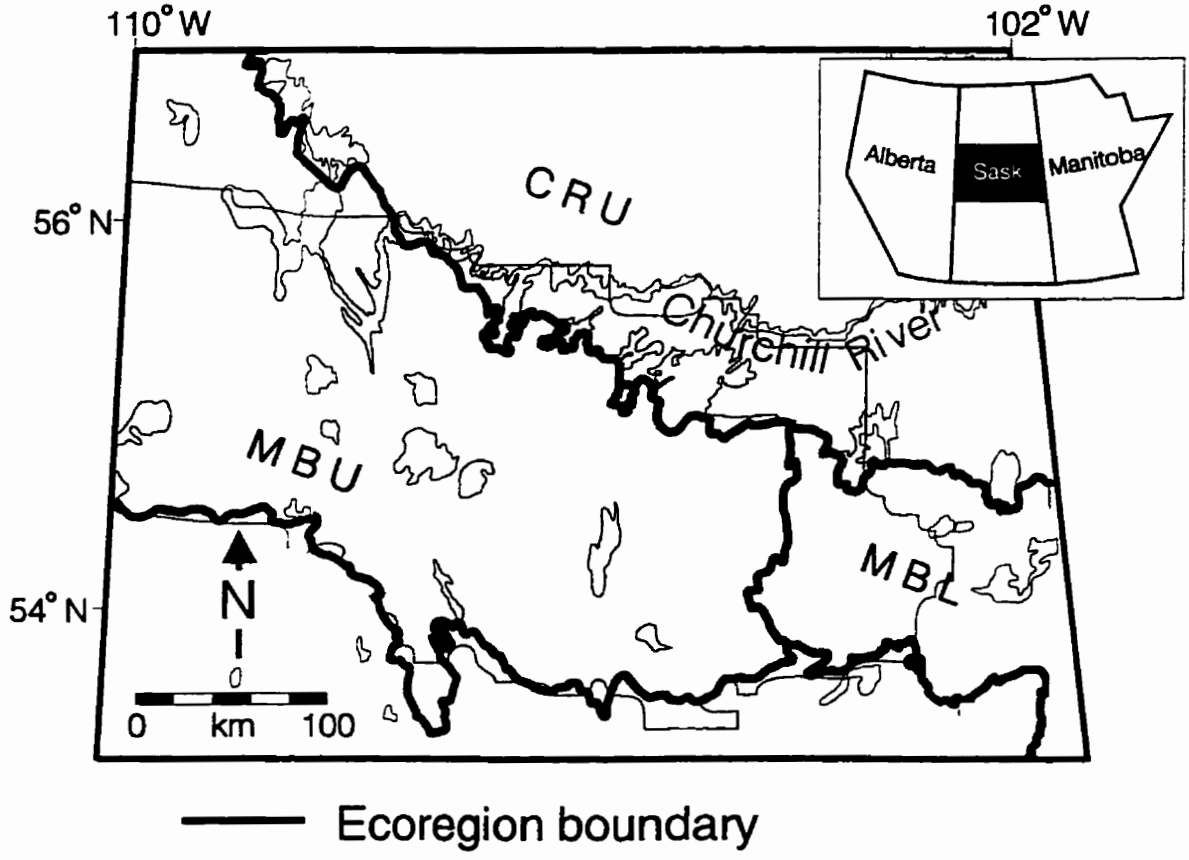

Fig. 1.1 The study area (shaded) is the Mid-Boreal Upland (MBU) ecoregion and adjacent portions of the Mid-Boreal Lowland (MBL) and Churchill River Upland (CRU) ecoregions within Saskatchewan. Inset shows the location of the larger map in Saskatchewan (Sask).

identification and description of vegetation communities available to woodland caribou in central Saskatchewan, owing to their importance as the currencies by which use and availability are measured (Chapter 2). The approach I employed involved stratified random sampling to quantify the vegetation in a variety of types of forest stands. The variables measured and the analytical techniques employed were chosen to meet my objective of describing habitat from an ungulate's perspective. I used canonical correspondence analysis to meet the second objective of my work on habitat description: to test the hypothesis that vegetation communities can be reliably inferred from data in the provincial government forest inventory, the most detailed vegetation classification system that encompasses my entire study area.

In ecological time, the value of habitat selection or any other behaviour can be measured by how it affects the demographic parameters of a population. In Chapter 3 I defined the populations of caribou in the study area from sets of radio-telemetry locations obtained for 40 adult female caribou between March 1992 and May 1996. I used data from radio-collared individuals to test the hypotheses that there were no differences in pregnancy, natality, and mortality rates; either among years, populations, or ecoregions. Data from aerial surveys were used to test for patterns in recruitment rates. At the regional level, I

calculated a rate of increase for the metapopulation to determine if caribou numbers were increasing or declining. I used demographic information to assess the factors limiting caribou populations in the region.

Finally (Chapter 4), radio-telemetry data were used to determine if woodland caribou in central Saskatchewan were selective in their use of habitat. I predicted that caribou would select habitat types to avoid the factors actually or potentially limiting the populations. The patterns of habitat selection were assessed at two spatial and temporal scales with respect to the vegetation communities described in Chapter 2. Selection was related to human disturbance in the region and to the limiting factors discussed in Chapter 3.

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2. IDENTIFICATION AND DESCRIPTION OF FORESTED VEGETATION COMMUNITIES AVAILABLE TO WOODLAND CARIBOU: RELATING WILDLIFE HABITAT TO FOREST COVER DATA

2.1. Introduction

Both government and industry have identified woodland caribou (*Rangifer tarandus caribou*) as a species whose preservation will affect forest management in central Saskatchewan (Rock 1992). My research into habitat selection by caribou began in 1992, and a primary requirement for any such research is the identification and description of relevant habitat types.

The diet of caribou in forested areas has been examined in many studies (*e.g.*, Edwards and Ritcey 1960; Edwards *et al.* 1960; Bergerud 1972; Miller 1976; Bloomfield 1980; Darby and Pruitt 1984; Cumming and Beange 1987; Servheen and Lyon 1989; Seip 1990; Racey *et al.* 1991). Generally, the literature reports that the spring diet consists of newly emerged green forage including graminoids, horsetails (*Equisetum* spp.), forbs, and leaves of deciduous shrubs. From summer through autumn, woodland caribou utilize sedges (Cyperaceae), grasses (Poaceae), horsetails, forbs, deciduous shrubs, and fungi. Autumn and

early winter are marked by a transition to increased use of arboreal and terrestrial lichens, and evergreen shrubs. In late winter, terrestrial lichens may be the most important food source. If snow depth or hardness impairs access to terrestrial lichens, arboreal lichens are likely to become the primary food item, as has been observed in both boreal and mountainous environments. Woody browse is generally a minor dietary item for caribou, and ingestion may be accidental (Edwards and Ritcey 1960; Bergerud 1972). Knowledge of vegetation in the understorey strata is therefore vital when characterizing caribou habitat.

In addition to representing available forage, overstorey and understorey vegetation affect other variables important to caribou. Habitat selection by cervids may be related to exposure to predation risk (*e.g.*, Bergerud *et al.* 1984; Bergerud 1985; Bergerud and Page 1987), insect avoidance (Downes *et al.* 1986; Walsh *et al.* 1992), snow cover (LaPerriere and Lent 1977; Brown and Theberge 1990) and summer thermal cover (Schwab and Pitt 1991; Schmitz 1991; Demarchi and Bunnell 1993). Vegetation affects relevant microhabitat characteristics like wind speed, light penetration, visibility, and snow accumulation. It also represents available forage for other species (*e.g.*, moose) that may share common predators. As a result, vegetation community types are the best method of characterizing caribou habitat.

2.1.1 Existing descriptions of vegetation in the region

Swan and Dix (1966) discussed associations between overstorey and understorey vegetation near Candle Lake, Saskatchewan. Their analyses were based on the frequencies of understorey vascular plant species in stands with homogeneous and tightly closed canopies. They concluded that shade cast by the forest canopy was of particular importance to understorey development. Other objective descriptions of plant communities in the southern boreal forest of Saskatchewan have been limited to further analyses of the same data (Dix and Swan 1971) and to descriptions of wetlands in the region (Jeglum 1972; 1973).

Based on data from subjectively selected plots, Kabzems *et al.* (1986) provided good descriptions of major plant communities found throughout the region. They used soil drainage and canopy species association to separate community types *a priori*. As a result, the number of communities recognized, their descriptions, and the understorey - canopy affinities presented were not derived objectively.

A comprehensive description of vegetation stands throughout the southern boreal forest in Saskatchewan has been created by the Forestry Branch of Saskatchewan Environment and Resource Management (Forestry Branch). The Forestry Branch has confined its efforts to an assessment of canopy species for the purpose of producing forest

inventory maps. Owing to the importance of understorey strata, all of the information relevant to caribou cannot be obtained directly from forest cover data. Communities with similar understorey attributes may relate to different overstorey types.

2.1.2 Forest cover data as wildlife habitat indicators

Forest inventory systems are similar in all provinces in Canada and have traditionally been created with the objective of measuring merchantable timber (Leckie and Gillis 1995). The use of forest cover data for purposes other than commercial forest management was not intended and may be inappropriate. Regardless of their intended use, forest inventory systems are often employed for habitat characterization in wildlife studies because they represent the most detailed vegetation descriptions available for large areas (Leckie and Gillis 1995).

Many studies have employed forest cover data to group forest stands into wildlife habitat types based on preconceived similarities (*e.g.*, Darby and Pruitt 1984; Cederlund and Okarma 1988; Leptich and Gilbert 1989; Hellegren *et al.* 1991). Others have later attempted to justify these groupings by collecting vegetation data from representative stands and presenting them as habitat descriptions (*e.g.*, Schwab and Pitt 1991; Boileau *et al.* 1994). The appropriate method is to derive habitat types

from vegetation data, rather than to define the types first and to then collect data to describe them.

Multivariate techniques, such as the ones I employ here, permit an assessment of the degree of correspondence between forest inventory data and independently determined community types. I feel this technique has the potential of creating a level of confidence in wildlife habitat descriptions based on forest inventory data.

The first objective of this study is to identify and describe vegetation communities derived from measurements of variables assumed to be important for woodland caribou. My second objective is to test the hypothesis that the vegetation communities I describe are correlated with the overstorey data maintained by the Forestry Branch. The description of vegetation communities and an assessment of the ability to predict community composition from available overstorey data represent the first steps in my research into habitat selection by woodland caribou in Saskatchewan.

2.2. Methods

2.2.1 Study area

The study area (Fig. 2.1) lies between approximately 53°30'N and 56°00'N and 104°00'W to 110°00'W. It is entirely within the Mid-Boreal Upland Ecoregion (Ecological Stratification Working Group 1995). Topography is mainly undulating to rolling plains of glaciolacustrine and

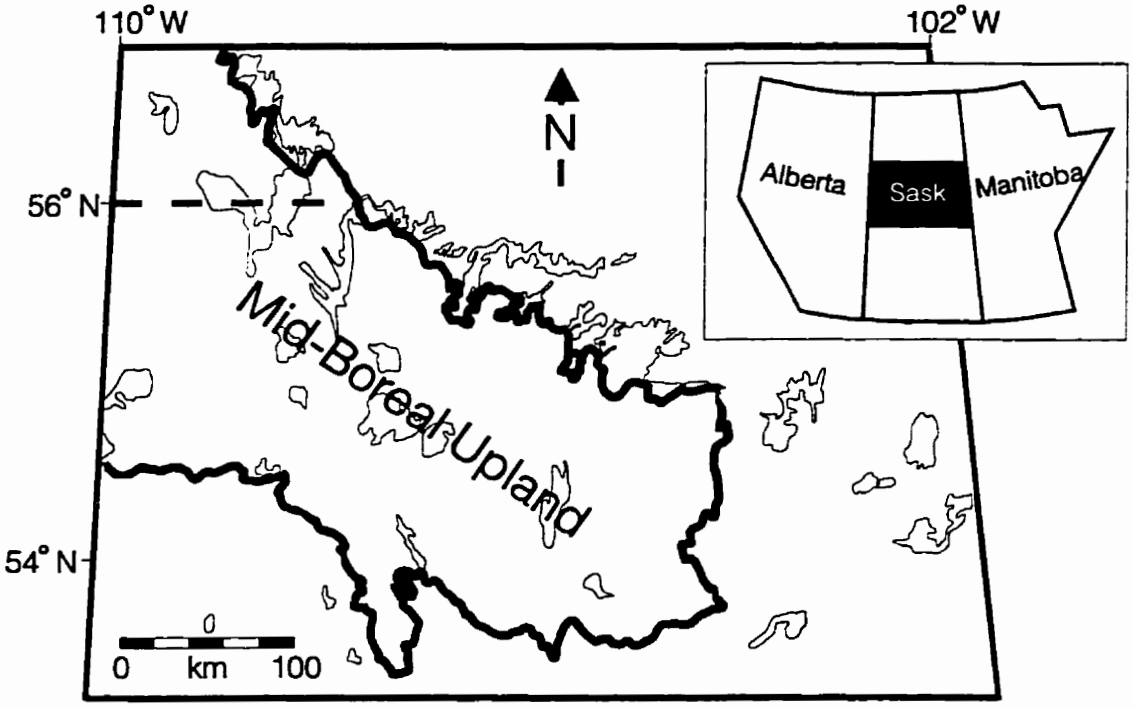

Fig. 2.1 The study area is the Mid-Boreal Upland ecoregion within Saskatchewan (the dashed line is the approximate northern limit of sampling). Inset shows the location of the larger map in Saskatchewan (Sask).

glaciofluvial origins (Harris *et al.* 1989). The climate is cool and subhumid with mean January and July temperatures of -19°C and +16°C, respectively. Mean annual precipitation is 45.6 cm, including a mean snowfall of 147 cm (Atmospheric Environment Service 1993).

Vegetation in the area is subject to frequent fires, integral features of the boreal forest that are responsible for much of the biodiversity in the region (Rowe 1970; Rowe and Scotter 1973). Dominant tree species are white spruce (*Picea glauca*), black spruce (*P. mariana*), jack pine (*Pinus banksiana*), and aspen (*Populus tremuloides*). Other important species are balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), tamarack (*Larix laricina*), and balsam poplar (*Populus balsamifera*).

2.2.2 Stand definition and selection

Due to the size of the study area (ca. 100 000 km^2), I adopted a stratified random sampling design. The Forestry Branch maintains a database in which all stands in the area that exceed approximately 4.0 ha are classified. Each stand is identified by the dominant tree species, degree of crown closure (where A = 10-30%, B = 30-55%, C = 55-80%, and D = 80-100% closure), height (in 5-m classes), and age (estimated decade of origin).

For each tree species or combination of species, Kabzems *et al.* (1986) quantified the area within the region

that was covered by each of the four categories of crown closure in each of four broad age classes. Ages of stands in each of the four age categories vary with canopy species, and the reader is referred to Kabzems *et al.* (1986, p.18) for exact values. With 16 combinations of age and crown closure for each canopy species (or combination of species), this method produced 208 different stand types.

My initial step was to define and select stand types to be sampled. For each canopy species (or species association), I combined the A and B closure classes and the C and D closure classes. I defined age classes using the ranges provided by Kabzems *et al.* (1986). The two oldest age classes were combined for each canopy type, further reducing the total to 78 stand types. From figures provided by Kabzems *et al.* (1986) I calculated total area covered by each of the 78 types. Each category comprising ≥1.0% of the total forested area in the region was included in the sampling schedule. One stand type (30 to 60-year-old aspen with canopy closure <55%) comprised 1.3% of the region by my calculations, but when the examination of 300 random locations failed to yield a single stand, it was excluded. The "treed peatland" category included in the Forestry Branch database was added, and I recognized a total of 21 stand types (Table 2.1) for sampling. I did

Table 2.1 Forest inventory attributes of stand types sampled.

Canopy species		Crown	Age	Stands
Primary	Secondary	closure*	(years)	sampled
Treed peatland†				3
Black spruce		+	>100	3
Black spruce		-	50-100	3
Black spruce		+	50-100	4
Black spruce		+	<50	4
Jack pine	Black spruce	+	>80	3
Jack pine	Black spruce	+	50-80	3
Jack pine		+	>70	4
Jack pine		-	40-70	3
Jack pine		+	40-70	3
Jack pine		-	<40	3
Jack pine		+	<40	3
White spruce		+	>70	3
Spruce‡	Aspen	+	>70	3
Spruce‡	Aspen	-	>70	4
Aspen	Spruce‡	+	>60	4
Aspen	Spruce‡	-	>60	3
Aspen		-	>60	3
Aspen		+	>60	4
Aspen		+	30-60	4
Aspen		+	<30	3

* Crown closure presented as greater (+), or less than (-) 55%.

† No age or closure attributes are attached to this category in the provincial forestry database.

‡ Any of: White spruce, black spruce or a combination of the two.

not differentiate between stands of fire versus logging origin.

Roads appearing on 1:250 000 topographic maps of the study area were divided into 500-m segments, and randomly selected road segments were located on 1:12 500 forest inventory maps. Though roads are not constructed at random, the prior selection of specific stand types for sampling should remove the bias associated with road location. Sample stands were selected such that they occurred within 1 km of the roadway within the selected segments. When a selected stand was found to have been logged or burned in the interval between mapping and my field work, an alternate stand was selected for sampling.

2.2.3 Field sampling

Sampling was conducted 18 June - 19 July 1993, and 7 June - 1 August 1994. In order to describe vegetation communities relevant to woodland caribou, I collected data on all vegetation strata, including arboreal lichens. The sampling procedure was hierarchical (Fig. 2.2).

A grid was drawn on the map to divide the stand into 50-m x 50-m sites, and three of the sites falling entirely within the stand boundaries were selected randomly for vegetation sampling. One corner of each site was located as accurately as possible using 1:12 500 forest inventory maps, a global positioning system unit, hip chain, and

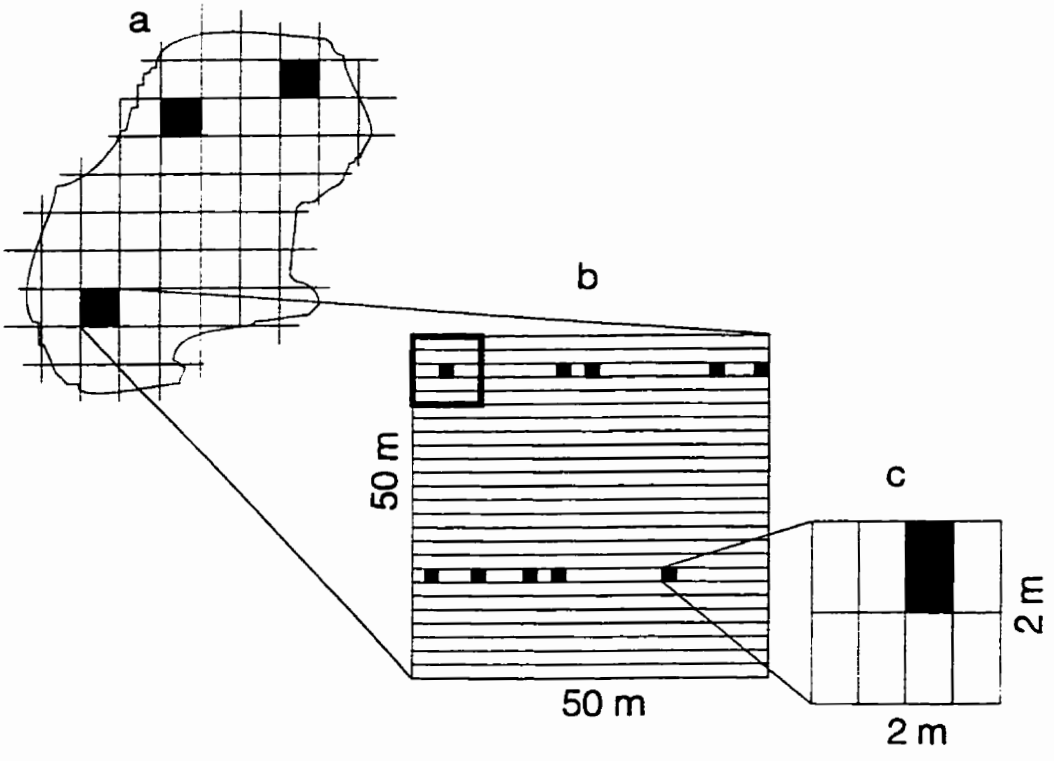

Fig. 2.2 Example of hierarchical sampling procedure showing selection of: a) sites (50-m x 50-m) within a stand; b) shrub (solid squares, 2-m x 2-m) and tree plots (open square, 10-m x 10-m) within a site; and c) a herb and dwarf shrub plot (0.5-m x 1.0-m) within a shrub plot.

compass.

Each site was divided into 25 2-m wide belts running east-west and two were randomly selected for sampling. On each of the two belts, five 2-m x 2-m plots were randomly selected, and percent cover was determined for shrubs (woody plants 0.5 to 5.0 m in height). Within each of the shrub plots, one of the eight possible 0.5-m x 1.0-m plots was selected randomly and percent cover was determined for rock, litter, water, bare soil, fungi, herbaceous vegetation, dwarf shrubs (woody plants ≤0.5 m in height), and bryophytes and lichens (as included in Table 2.2). Common Labrador tea (*Ledum groenlandicum*) was always considered to be a dwarf shrub, though it frequently exceeded 0.5 m in height.

One of the 25 potential 10-m x 10-m plots in the site was randomly selected such that it contained at least one of the shrub plots. This plot was used to assess tree cover. While trees were normally considered to be woody plants ≥5.0 m tall, an exception was made in young stands that forest inventory maps indicated had a canopy 5.0 ± 2.5 m in height. In those stands, an individual was considered a tree upon reaching 2.5 m.

In all cases, percent cover was determined by visual estimation. The cover-class scale I used was first described by Bailey and Poulton (1968) and has seven

categories: 0-1% ; 1-5% ; 5-25% ; 25-50% ; 50-75% ; 75-95% ; and 95-100%.

In each tree plot, the total number of live and dead individuals was determined for each species, a visual assessment of crown closure was made (using the four crown closure classes described previously), and a core sample was taken from one randomly selected tree of each of the nominal species for aging. Arboreal lichens were sampled from randomly selected trees (one live and one dead tree of each species found within each tree plot). Live and dead trees were considered separately as they have been found to support different quantities of arboreal lichens (Rominger *et al.* 1994). Selection of sample branches and methods of collection followed Van Daele and Johnson (1983) with the exception of height intervals. Height intervals were 1-2, 2-3, and 3-4 m in the 20 stands sampled in 1993, and were revised to 0-1 and 1-2 m for the 50 stands sampled in 1994. The revision followed an assessment of snow depth in the winter of 1993-94. Unlike conditions elsewhere (*e.g.*, Edwards *et al.* 1960), snow depths in my study area do not normally exceed 50 cm and do not give caribou a platform from which to browse at greater heights. Calculations for biomass were based on the assumption of the 0-2 m segment of each tree being accessible throughout the winter.

In summary, sampling was conducted in a total of 70 stands, containing 210 10-m x 10-m plots, 2100 2-m x 2-m

plots, and 2100 0.5-m x 1.0-m plots. Nomenclature follows Moss (1983) for vascular plants, Hale (1979) for lichens, and Crum (1983) for mosses. Voucher specimens of vascular plants have been deposited with the W.P. Fraser Herbarium, University of Saskatchewan, Saskatoon.

2.2.4 Laboratory analyses and data preparation

Tree cores were mounted, sanded, and aged by counting annual rings with the aid of a dissecting microscope. Arboreal lichens were stripped from sample branches by hand, air dried in paper bags and later oven dried for 1 hour at 50° C immediately prior to being weighed to the nearest 0.0001 g. The biomass of lichens for each species of tree was calculated separately for each stand after the methods of Van Daele and Johnson (1983). Total arboreal lichen biomass for the stand was obtained by adding the values for all the tree species sampled. These were then converted to kg/ha.

Cover-class values for each taxonomic group (usually species) were pooled to produce a single percent-cover value for each site based on midpoint values for each class (Bailey and Poulton 1968). Following the procedure used by Carleton and Maycock (1981), percent cover for each taxonomic group in each height stratum was considered as an independent variable. Mean values from the three sites in

each stand were later pooled to provide a single set of values for each stand.

Taxonomic groups rare in abundance or occurrence were eliminated from analyses according to the following criteria: (1) when a taxon failed to attain a minimum pooled value of 0.5% cover in a site it was entered into the database as 0; (2) following the pooling of data for each stand, all cover values <0.5% in the stand were reduced to 0; and (3) any taxon that did not attain 1.0% cover in >5% of the stands (*i.e.*, at least 4 of the 70 stands) was excluded from analyses.

A reduced version of the data set was produced by deleting deciduous understorey taxa along with herbaceous taxa whose shoots do not remain erect after the growing season. This data set was taken to represent the vegetation available in winter. The main data set is hereafter referred to as the "summer" data while the reduced data set is referred to as the "winter" data. Data transformations and analyses described below were conducted separately on each set of data.

2.2.5 Data standardization and analyses

Data standardization was required because three different units of measure were employed (Noy-Meir *et al.* 1975). Within each of the three measures (biomass, percent cover, and stem counts), the maximum value observed among

all taxa was used to standardize the data. Data were standardized by dividing each score by the maximum value observed for the measure. This permitted the retention of relative abundances among taxa within each measure, while placing all values on equivalent scales. Data were then stand normalized (Orlóci 1967). Therefore, the Euclidean distance used for the classification and ordination procedures was chord distance (Orlóci 1967; van Tongeren 1987).

Both classification and ordination were used to identify and describe vegetation community types (Orlóci 1978). Classification was conducted using the sum of squares agglomerative clustering method (Ward 1963; Orlóci 1967) with the computer programme PC-ORD (McCune and Mefford 1995). The level at which clusters are recognized is subjective, based on changes in the sum of squares at each successive fusion, as well as on ecological considerations.

Ordination by nonmetric multidimensional scaling (NMDS, Kruskal 1964), specifying two to six dimensional solutions and Euclidian measure, was conducted with PC-ORD (McCune and Mefford 1995). Random starting configurations were used and analyses were repeated to avoid locally optimal solutions (Gauch *et al.* 1981). An optimal solution was considered to have been attained when 10 consecutive trials failed to produce an improvement in stress value.

Canonical correspondence analysis (CCA) was conducted (using the computer programme CANOCO version 3.12; ter Braak 1991) to determine the ability of data in the provincial forest inventory to predict vegetation community composition. I also used CANOCO to conduct correspondence analysis (CA) on the summer and winter data sets because CA is helpful in the interpretation of CCA results. Correspondence analysis functions to ordinate species and stand points such that the dispersion of species scores along each axis is maximized and the scores on higher axes are not correlated with scores on lower axes (ter Braak 1987). Canonical correspondence analysis imposes the additional constraint that species scores on each axis are linear combinations of data in a related data set. A comparison of results from both procedures provides a measure of how much information is lost by imposing the additional constraint of CCA (ter Braak 1986). When the variation explained through CCA is nearly equal to that explained through CA, then the related data set alone is sufficient to explain the major variations observed in the main data set. This is true even though the total variation explained may be low (ter Braak 1986).

The forest inventory data set I used to constrain CA scores for CCA was extracted from Forestry Branch maps. The set contained the following information: qualitative scores for each of the canopy tree species (where 2 =

primary, 1 = secondary, and 0 = absent); stand age; and stand canopy closure. Maps did not provide the necessary data for the three "treed peatland" stands, and field data were used, although the scores for tree species are not independent of the summer and winter data sets in these three cases. Each map variable was standardized to zero mean and unit variance prior to use in analyses (ter Braak 1987).

2.3. Results

The results of the analyses on the winter data set were largely comparable to those obtained for the summer data set. Only general results and a short description of the major divergences between summer and winter community types are presented. Winter data counterparts of Table 2.2 and Figures 2.3-2.5 appear in Appendix A.

2.3.1 Classification of stands

Cluster analyses suggested that seven classes of vegetation be recognized in summer (Fig. 2.3) and six classes in winter. Classification efficiencies (Orlóci 1978) were 57.8% for the summer data and 58.0% for the winter data.

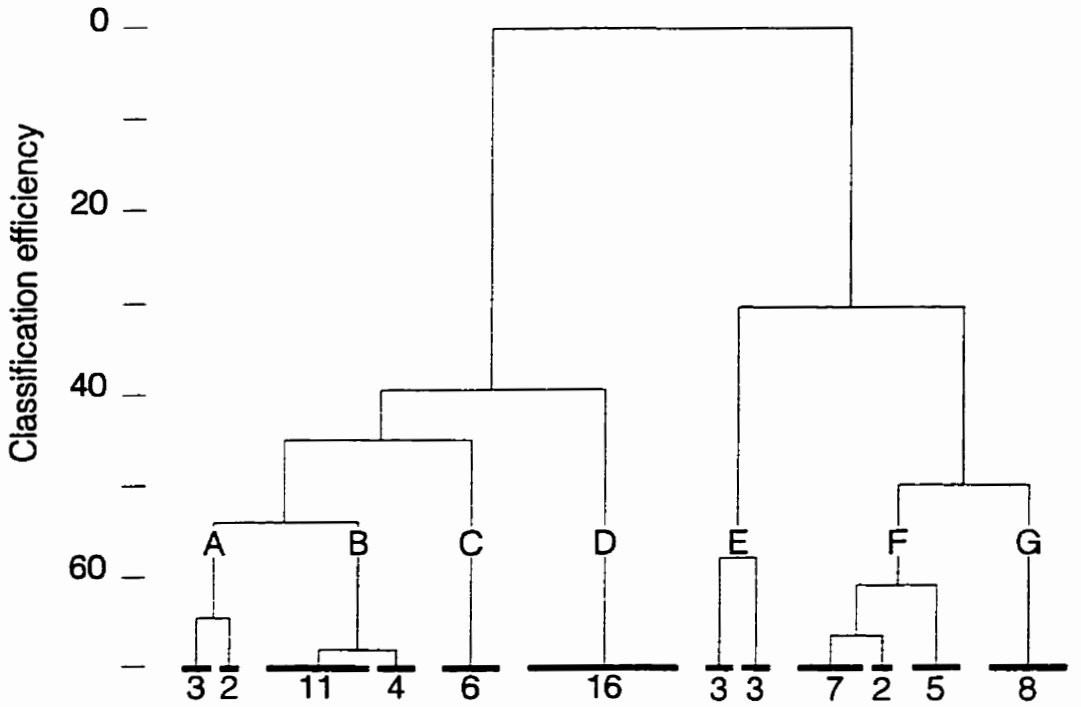

Fig. 2.3 Sum of squares classification dendrogram of the 70 stands based on summer data. The seven community types described in the text are indicated by the letters A-G. Numbers along the bottom of the figure indicate the number of stands contained in the corresponding branches.

Each of the communities is described below and has been named following its dominant canopy and understorey components. Descriptions are based on summer vegetation (Table 2.2).

Type A: *Vaccinium vitis-idaea - Cladina mitis - Pleurozium schreberi*

Classification placed two distinct stand types into community type A. Both stand types contain large amounts of the three characteristic species as well as lesser quantities of cup lichens (*Cladonia* spp.) and foliose lichens (*Peltigera* spp.), but diverge in quantities of other species present. Both variants of this community also contain large amounts of arboreal lichen relative to most communities described.

A1: *Pinus banksiana - Vaccinium vitis-idaea - Cladina mitis - Pleurozium schreberi*

This variant is found on very dry sites beneath jack pine stands of <55% canopy closure and >40 years in age. The shrub layer is poorly developed and is primarily green alder (*Alnus crispa*). The herb and dwarf shrub vegetation layer consists of the ericaceous shrubs: bog cranberry (*Vaccinium vitis-idaea*), common bearberry (*Arctostaphylos uva-ursi*), and blueberry (*Vaccinium myrtilloides*). Ground cover is predominantly yellow reindeer lichen (*Cladina*

Table 2.2 Mean vegetation characteristics of the seven summer plant communities determined by cluster analysis.

Taxon	Community						
	A	B	C	D	E	F	G
Trees*							
Abies balsamea		380		27			125
Betula papyrifera		31	211	173	17		50
Larix laricina	367	4			172		42
Picea glauca		358		87		5	21
Picea mariana	507	384	94	48	1522	1312	5142
Pinus banksiana	500	18	6133	42	856	1162	100
Populus balsamifera		22		144			
Populus tremuloides	27	249	467	1450	56	60	
Salix spp.			11	71		12	21
Shrubs†							
Abies balsamea		11.5		0.6			2.7
Alnus crispa	1.2	4.2	3.8	18.4	3.0	12.9	0.2
Alnus tenuifolia		0.3			0.2	0.5	0.1
Betula papyrifera	0.8	0.1	0.3	1.6	0.1	0.9	
Picea glauca	0.2	1.3	0.6	2.5			
Picea mariana	5.1	2.9	12.2	1.3	6.7	9.7	8.5
Pinus banksiana	0.4		4.1				
Populus tremuloides		0.8	2.8	3.2			
Prunus pensylvanica			0.2	0.6			
Rosa spp.	0.5	0.7		3.8	0.3	0.1	0.3
Rubus idaeus		0.8		1.5			
Salix spp.	2.8	0.9	3.2	2.2	1.5	0.8	0.1
Viburnum edule		0.4		4.4			
Herbaceous / Dwarf shrub†							
Abies balsamea	0.1	1.5		0.3			0.4
Alnus crispa			0.3	0.2		0.4	

Table 2.2 continued

Taxon	Community						
	A	B	C	D	E	F	G
Aralia nudicaulis	0.9	4.0		11.0	0.7	0.3	0.1
Arctostaphylos uva-ursi	3.8	0.3	1.9		0.3	2.2	
Aster spp.		0.2		1.0			
Chamaedaphne calyculata	1.7				4.4		
Cornus canadensis	1.8	3.5	1.2	6.5	0.8	1.2	0.9
Cyperaceae	0.6	0.2			3.5	0.2	0.5
Epilobium angustifolium		0.7	1.0	5.5	0.2	0.4	
Equisetum arvense		1.4		0.6	0.1		1.5
Equisetum pratense		0.6		0.3			0.1
Equisetum sylvaticum			0.9	0.2	0.1	0.4	2.6
Fragaria virginiana	0.2	0.3	0.2	1.6			
Galium boreale				1.0		0.1	
Lathyrus ochroleucus	0.2	0.3	0.2	2.6			
Ledum groenlandicum	13.1	4.9	10.6	1.9	11.3	11.8	11.2
Linnaea borealis	2.8	2.4	0.8	4.8	0.4	1.9	0.1
Lonicera involucrata		0.1		0.3			
Lycopodium annotinum		1.7	0.2	3.7		0.9	0.2
Lycopodium complanatum	0.7	0.2		0.2		0.3	
Maianthemum canadense	2.0	0.7	1.2	1.8	0.5	0.9	
Mertensia paniculata	0.1	1.3		2.3			
Mitella nuda		2.2		0.5			
Petasites palmatus		1.2	0.6	1.9	0.2		0.4
Picea mariana	0.3	0.4	2.8		0.3	1.1	0.7
Poaceae	3.7	1.0	2.5	14.2	2.2	1.0	0.6
Ribes triste		0.3		0.9			
Rosa spp.	0.7	1.0	0.5	3.8	0.7	0.3	0.5
Rubus chamaemorus	2.5				1.0	0.2	
Rubus idaeus		0.3		1.9		0.1	
Rubus pubescens	0.2	1.8		3.9	0.2	0.1	
Salix spp.	0.6		1.3	0.1	0.2		0.3
Smilacina trifolia	2.0				1.9	0.5	0.2

Table 2.2 continued

Taxon	Community						
	A	B	C	D	E	F	G
Symphoricarpos albus		0.1		0.7			
Trientalis borealis		1.0		1.0		0.3	
Vaccinium myrtilloides	4.2	0.9	19.6	2.8	2.4	5.9	0.5
Vaccinium vitis-idaea	11.4	1.3	3.0	1.0	3.5	5.3	1.6
Viburnum edule		0.9		2.8	0.1		0.1
Vicia americana	0.1			0.9			
Mosses and lichens[†]							
Cladina mitis	26.2	0.1	0.8		13.2	3.9	1.2
Cladina rangiferina	0.5	0.1			1.8	1.8	0.7
Cladonia spp.	2.1		2.9	0.1	1.5	0.4	0.1
Dicranum spp.	1.3	0.8	4.1	0.4	0.7	1.8	1.2
Hylocomium splendens	0.3	14.8		0.7	6.5	3.1	23.6
Peltigera spp.	2.2	0.6	3.1	0.1	0.4	0.4	1.3
Pleurozium schreberi	16.2	14.7	1.7	1.4	23.2	55.9	45.9
Polytrichum spp.		0.1	10.8	0.1	1.2	0.5	0.5
Ptilium crista-castrensis	0.2	2.9			1.7	3.6	5.4
Sphagnum spp.	5.4	0.1	1.8		22.3	0.8	3.3
Non-vegetative cover[†]							
Litter	67.7	76.0	72.8	94.7	37.3	52.0	46.3
Water	2.6	1.0	0.2	0.2	1.1	0.3	0.2
Arboreal lichen[‡]							
Total	35	9			97	25	19

[•] Tree cover expressed in stems/ha.

[†] Shrub, herbaceous, dwarf shrub, moss, lichen, and non-vegetative cover expressed in percent cover. Values <0.1% are not shown.

[‡] Arboreal lichen totals expressed in kg/ha.

mitis) with red-stemmed feathermoss (*Pleurozium schreberi*) being of secondary importance.

A2: *Picea mariana - Vaccinium vitis-idaea - Cladina mitis - Pleurozium schreberi*

The black spruce variant of this community is found in black spruce bogs and may include tamarack in the relatively open canopy (<45% closure). Black spruce provides a modest shrub layer while the lower strata are dominated by common Labrador tea and bog cranberry. Ground cover is provided by red-stemmed feathermoss, yellow reindeer lichen, and peat moss (*Sphagnum* spp.) in similar quantities.

Type B: *Picea glauca - Cornus canadensis - Hylocomium splendens / Pleurozium schreberi*

This community type is characterized by stands of all ages and closure classes in which the canopy is dominated by white spruce (frequently in combination with aspen and/or black spruce). Stands with mixed canopies dominated by black spruce (in combination with aspen and/or white spruce) are also part of community type B. Balsam fir is commonly present in a secondary canopy layer and as the dominant shrub. Below 0.5 m the important species found in most stands are wild sarsaparilla (*Aralia nudicaulis*), bunchberry (*Cornus canadensis*), twin-flower (*Linnaea*

borealis), stair-step moss (*Hylocomium splendens*), red-stemmed feathermoss, and knight's plume (*Ptilium crista-castrensis*). Arboreal lichens are not abundant.

Type C: *Pinus banksiana - Picea mariana - Vaccinium myrtilloides / Ledum groenlandicum*

This community type is found beneath a young (<40 year old) jack pine canopy of all closure classes. The shrub layer consists of jack pine, black spruce, and willow (*Salix* spp.). The layer below 0.5 m is dominated by blueberry and common Labrador tea with minor amounts of ground cover provided by hair-cap mosses (*Polytrichum* spp.) and foliose lichens. This community type contains virtually no arboreal lichens.

Type D: *Populus tremuloides - Alnus crispa - Aralia nudicaulis* / Poaceae

The overstorey of this type is dominated by aspen of all ages, occasionally combined with white spruce or jack pine. Canopy closure is >65%, though where stands have been selectively logged for white spruce, closure may be <45%. Total shrub cover is approximately 40% and is dominated by green alder, usually with rose (*Rosa* spp.) and / or low-bush cranberry (*Viburnum edule*). Herbaceous and dwarf shrub vegetation is abundant. Species found in most stands include grasses, wild sarsaparilla, bunchberry,

dewberry (*Rubus pubescens*), fireweed (*Epilobium angustifolium*), and twin-flower. Mosses, and terrestrial and arboreal lichens are all nearly absent in this community type.

Type E: *Picea mariana - Ledum groenlandicum - Pleurozium schreberi / Sphagnum* spp.

Typical stands are mature black spruce stands (>90 years old) with canopy closure of <55%. They are commonly found on poorly drained soils as evidenced by the presence of standing water, three-leaved Solomon's-seal (*Smilacina trifolia*), leather-leaf (*Chamaedaphne calyculata*), and peat mosses. This type also includes stands listed as being a mixture of black spruce and tamarack. The poorly developed shrub layer is dominated by black spruce. Common Labrador tea is the only species present in large amounts in the herb and dwarf shrub stratum though sedges, bog cranberry, and leather-leaf are also found in most stands. Ground cover is provided by red-stemmed feathermoss and peat mosses. Arboreal lichens are most abundant in this community type.

Type F: *Picea mariana / Pinus banksiana - Ledum groenlandicum - Pleurozium schreberi*

This community is most common beneath mixed jack pine / black spruce canopies. It also includes pure black

spruce stands of <55% cover and <90 years old. Jack pine stands of >40 years of age and >55% closure are also included in this community type. The shrub layer is dominated by green alder and/or black spruce. Ground cover by red-stemmed feathermoss is high in all stands. Common Labrador tea is the dominant species in a herb and dwarf shrub stratum where bog cranberry and blueberry are also abundant. Arboreal lichen availability is moderate.

Type G: *Picea mariana - Ledum groenlandicum - Pleurozium schreberi / Hylocomium splendens*

This community is found beneath pure black spruce stands of all ages and >55% canopy closure. Shrub and dwarf shrub / herbaceous layers are poorly developed, the former being largely black spruce and the latter dominated by common Labrador tea. Bryophyte abundance is highest in this community, with all stands containing large amounts of red-stemmed feathermoss and stair-step moss, and lesser amounts of knight's plume.

There were two important differences in the classification of the winter data: summer community types F and G were combined into one cluster; and the stands from the *Picea mariana - Vaccinium vitis-idaea - Cladina mitis - Pleurozium schreberi* variant of summer community type A were grouped with community type B. Four other stands

changed clusters, with negligible effects on mean abundances of species in the affected communities.

2.3.2 Ordination of stands

For each data set I plotted the stress values that resulted from NMDS against the specified number of dimensions. In both cases the inflection points in the plots supported the use of three dimensional solutions.

For the summer data set (Fig. 2.4) it was necessary to plot the third dimension in order to distinguish between community types A and E, and to separate types A and E from types B and D. The overlap of community types F and G was less in the second dimension than in the third dimension, but the ordination failed to provide a clear distinction between the two types, indicating that they might best be considered as a single type. The solution obtained had a stress value of 9.7%. The ordination of winter data (Fig. A.2) confirmed that types F and G be considered as a single community type, as suggested by the classification. The winter solution had a stress level of 8.5%.

Although the two NMDS ordinations and the winter classification indicate that community types F and G are a single community, I will continue to refer to them independently for the purposes of discussion.

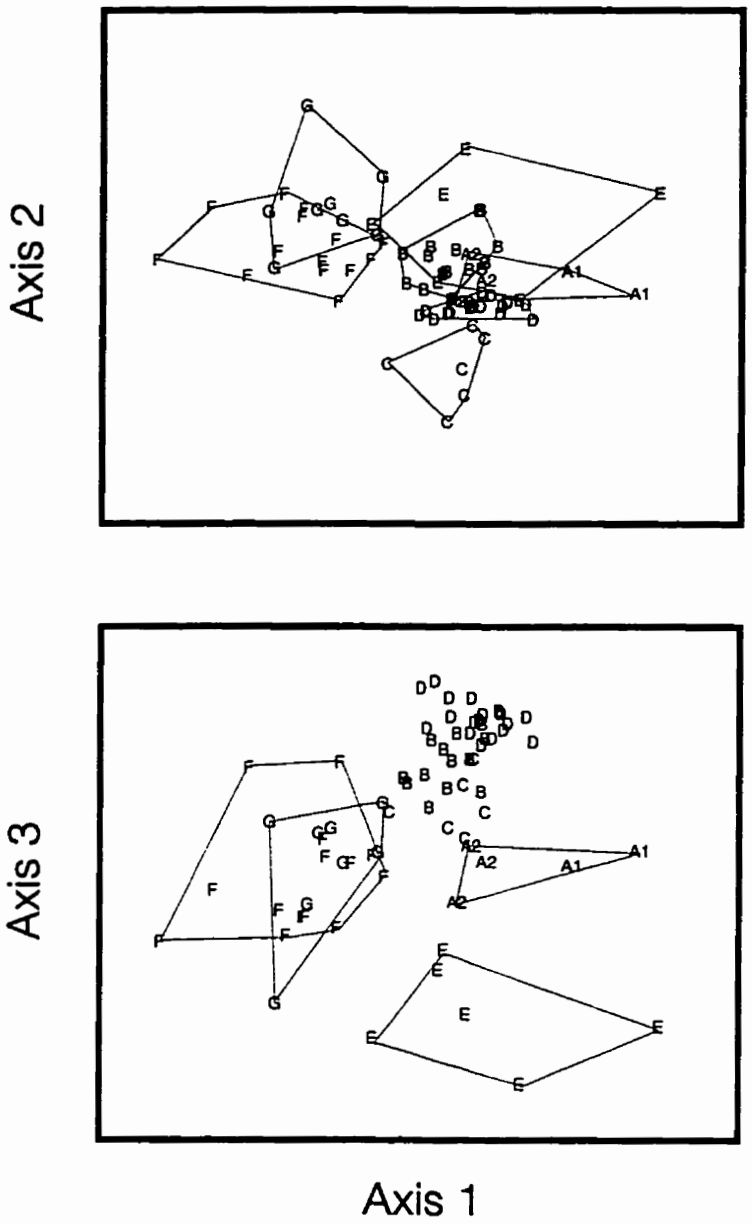

Fig. 2.4 Nonmetric multidimensional scaling ordination of the 70 stands based on summer data. The letters A-G represent community membership identified by classification (Fig. 2.3) and described in the text.

2.3.3 Canonical ordination of stands

The variation in vegetation community data explained by linear combinations of Forestry Branch data (CCA results) was high relative to the variation observed in the CA of community data (Table 2.3). The correspondence between CA and CCA results was slightly higher for the winter data set, and the plots of the winter ordination were remarkably similar to those for the summer data set.

An arch effect (Gauch *et al.* 1981) was observed on the third axis of CA and CCA plots so I have plotted the canopy vectors and the stand types in only two dimensions (Fig. 2.5). The first CCA axis shows a strong contrast between stands dominated by aspen (type D stands) and those dominated by black spruce (types E, F, and G). This dichotomy is clearly evident in the orientation of the species vectors (Fig. 2.5).

The species vectors also show a polarity between white spruce (type B stands) and jack pine (stand types A and C). There was a positive correlation between the age vector and the second axis for each season. The correspondence between CA and CCA, 86% on the first axis, declined to 71% for the second axis (Table 2.3). This decline may be due to the relationships between the second axes and age, a difficult parameter to estimate from air photos. Total correspondence between CA and CCA on the first two axes was 80%, indicating that the data in the

Table 2.3 Variation (%) in summer vegetation explained by the first two axes of correspondence analysis (CA) and canonical correspondence analysis (CCA).

	Variation
Axis 1	
CA	15.3
CCA (%CA)	13.1 (86%)
Axis 2	
CA	10.3
CCA (%CA)	7.3 (71%)
Totals	
CA	25.6
CCA (%CA)	20.4 (80%)

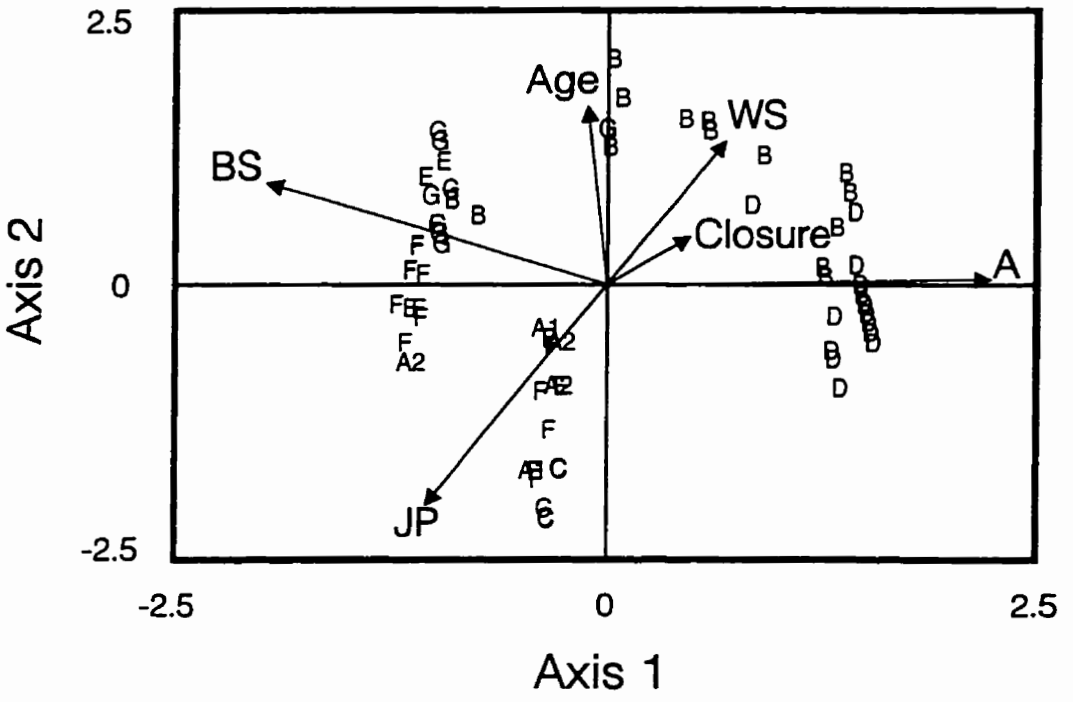

Fig. 2.5 Biplot of canopy characteristics and stand types on the first two canonical correspondence analysis axes for summer data. The letters A-G represent community membership identified by classification (Fig. 2.3) and described in the text. Canopy vectors are for age, closure, White spruce (WS), black spruce (BS), jack pine (JP), and aspen (A). Vector lengths shown are 2.5 x original values.

forest inventory are adequate to explain 80% of the variation observed in the sample stand data.

2.4 Discussion

Multivariate analyses were successful in identifying vegetation communities in my study area. While the results from NMDS tend to support the communities derived in cluster analyses, the relationships of stands within and among some communities are not immediately obvious. The lack of obvious relationships highlights the problems that may arise from grouping stands based on preconceived similarities. For community types to be meaningful it is fundamental that they be ecologically interpretable. Section 2.4.1 considers community types and their successional relationships. It is organized by primary canopy species.

The results obtained through CA and CCA were less clear in their ability to separate community types, but the objective in using CCA was to assess the relationship between vegetation community and overstorey characteristics found on forestry maps. This relationship is discussed in section 2.4.2.

2.4.1 Successional relationships and community types

Pinus banksiana

Jack pine community types in my classification scheme are primarily divided by age, a finding similar to that of Carleton and Maycock (1981). Community type C appears to be an early seral stage common to all jack pine stands. Like Kenkel (1986), my results do not suggest a single successional sequence for upland jack pine sites. My cluster analyses placed stands from well drained sandy sites into community type A1 (*Pinus banksiana - Vaccinium vitis-idaea - Cladina mitis - Pleurozium schreberi*), a community that may be sustained by frequent fires (Desponts and Payette 1992). Other jack pine stands are found in community type F as a *Pinus - Ledum - Pleurozium* association, and are apparently progressing towards my *Picea mariana / Pinus banksiana - Ledum groenlandicum - Pleurozium schreberi* community (also type F). The results from CCA analyses tend to support the successional sequences outlined above. From the location of type C stands in Fig. 2.5, the bearing of the age vector leads to the general locations of stands from community types A1 and F.

Populus tremuloides

Community type D contains all stands with pure aspen canopies plus those stands where white spruce exists as a

suppressed secondary layer. All stands contain dense and varied understorey flora similar to the aspen stands described in other studies (Dix and Swan 1971; Corns 1983; Kabzems *et al.* 1986). The allegiance of aspen stands to a single community type, regardless of closure and age, is also consistent with the findings of Carleton and Maycock (1981). In the absence of fire, the fate of type D communities appears to be gradual succession to type B communities. Successional stands would be dominated by white spruce, or occasionally by black spruce (Rowe 1956; Swan and Dix 1966; Archibold 1980; Van Cleve and Viereck 1981; Corns 1983; Kabzems *et al.* 1986). Canonical correspondence analysis results (Fig. 2.5) show that from type D stands, the bearing of the age vector leads to type B stands as would be expected.

Picea glauca

All stands dominated by white spruce fall within community type B. As discussed above, origins of stands in this community type are commonly type D communities. A less common origin would be situations where a stand of white spruce was able to replace itself following disturbance (Kabzems *et al.* 1986). Where white spruce and black spruce are both found in the canopy, succession to black spruce alone is likely. The CCA results suggest that among type B stands, an increase in the value on axis two

(corresponding with an increase in age) generally coincides with a lower value on axis one (corresponding with a decline in aspen and/or an increase in black spruce).

Picea mariana

The primary bifurcation in the dendrogram (Fig. 2.3) splits the black spruce community types from those dominated by any other species. Black spruce communities are more numerous and complex than all others in the classification. The initial division among black spruce community types is by degree of canopy closure (either greater or less than 55% closure), a feature that is similar to the findings of Carleton and Maycock (1981).

Community types F and G both contain stands in which black spruce appears to have been the pioneer tree species following fire. Black spruce is also an important understorey species in all but the driest jack pine stands (Dix and Swan 1971). The majority of stands in type F appear to be upland stands that are in transition from jack pine / black spruce types to the pure black spruce stands of community type G, as observed elsewhere (Carleton and Maycock 1978; Kabzems *et al.* 1986). The understorey composition of type F and G stands support the observation that closed canopy black spruce stands seem to proceed towards the elimination of everything except feathermosses (*e.g.*, Carleton and Maycock 1981; Van Cleve and Viereck

1981; Johnson 1981). Type G stands are generally found with higher axis two values than type F stands (Fig. 2.5), suggesting greater age and supporting the argument that they are a later successional stage. Winter cluster analysis and summer and winter ordination results suggest great similarity between community types F and G, indicating that they should possibly be considered a single community type.

Community types A2 and E are comprised of lowland black spruce stands. Species and nutrient-rich tamarack fens are the likely precursors to both types. The succession of fens by black spruce bogs occurs when the peat layer thickens and isolates roots from nutrient rich waters (Jeglum 1972; 1973; Rowe and Scotter 1973; Zoltai *et al.* 1988). Jeglum (1972) described a *Picea mariana / Ledum groenlandicum / Sphagnum* spp. peatland as a younger form of a *Picea mariana / Ledum groenlandicum / Pleurozium schreberi* peatland. Both types would likely fit within the type E community described above, and succession is dependent upon continued accumulation of peat (Jeglum 1973).

At the later stages of development in all bog types, reindeer lichens (*Cladina* spp.) can become abundant on peat moss hummocks (Jeglum 1972; Van Cleve and Viereck 1981; Zoltai *et al.* 1988). This may produce a community similar to my *Picea mariana - Vaccinium vitis-idaea - Cladina mitis*

/ *Pleurozium schreberi* community (type A2). The relationship of type A2 to type A1 is low nutrient availability and a relatively open canopy. Wet depressions or hollows account for the presence of peat mosses in type A2 stands.

2.4.2 Relationships between community types and canopy types

Canonical correspondence analysis showed that canopy features were able to explain 80% of the variation in the species data and suggests a strong relationship between canopy and understorey vegetation. Furthermore, the results suggest that the community types I have described can be distinguished by overstorey characteristics.

Canopy species should relate to edaphic conditions at the time of their arrival at the site. In general the canopy species are dependent upon specific ranges of soil moisture (Rowe 1956; Dix and Swan 1971). Carleton and Maycock (1981) found that the limited number of understorey species with specific canopy affinities shared edaphic requirements with the tree species. Kenkel (1986) stressed the importance of soil moisture in dictating understorey species composition in jack pine stands in Ontario.

Understorey flora must also be adapted to light characteristics associated with specific tree species and differing degrees of canopy closure (Carleton and Maycock

1981; Ross *et al.* 1986). The relationships among succession towards a closed coniferous canopy, increases in bryophyte abundance and soil moisture, and decline in vascular plant performance have been widely reported (Rowe 1956; Swan and Dix 1966; Ross *et al.* 1986). Ross *et al.* (1986) found that unlike the conditions in coniferous stands, dense aspen canopies show marked seasonal changes in leaf structure and colour. These changes may provide an annual range of light conditions sufficient to inhibit bryophytes and permit the persistence of a dense vascular understorey. Integrity in forest plant communities is best characterized by the functional dependence between canopy and understorey (Carleton and Maycock 1981).

2.4.3 Conclusion

By selecting relevant variables and using them to derive vegetation communities, the communities I describe should relate to those perceived by caribou. My CCA results are an indication of the high correlation between canopy characteristics and communities defined by both overstorey and understorey vegetation. As a consequence, the community types I describe are strongly related to the types of information contained in the Forestry Branch data base. The results support the use of forest inventory data to infer vegetation community types in my study of caribou habitat selection. More generally, I demonstrate how the

use of multivariate techniques to assess correspondence between related data sets can validate the use of forest cover data for broader ecological purposes.

The real test of the relevance of the community types delineated for any wildlife species will be whether or not they relate to habitat selection by individuals. This is the focus Chapter 4, where I report on the use of satellite radio-telemetry to track caribou in the study area.

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3. DYNAMICS OF WOODLAND CARIBOU POPULATIONS AT THE SOUTHERN LIMIT OF THEIR RANGE IN SASKATCHEWAN

3.1 Introduction

Throughout North America, the decline of woodland caribou (*Rangifer tarandus caribou*) has followed human settlement (Bergerud 1974). Reductions in caribou populations and their ranges are continuing as human activity erodes the margins of their distribution (Edmonds 1991). As a consequence, woodland caribou is listed as a vulnerable species in western Canada. The expansion of forestry, and of activities associated with oil and gas exploration and extraction is further threatening caribou in the southern portions of their range in Saskatchewan. If resource management in the area is to include the conservation of viable woodland caribou populations then it is fundamental that basic demographic data be available.

Existing data on woodland caribou in central Saskatchewan were summarized by Rock (1992) and are largely limited to success rates of licensed hunters, beginning in 1966 when the first pulp mill was opened and road networks were constructed in the forest. Hunting success peaked in the early 1970s then fell sharply, suggesting a decline in

the caribou population. Low levels of hunter success lasted for more than 10 years, until 1986 when licensed hunting was stopped entirely. Local knowledge suggests that caribou populations declined or disappeared in many areas following the increase in logging activity (Trottier 1988). These declines may be related to many factors including licensed and subsistence hunting, severe winters, habitat alteration, and the end of a programme to control wolves (*Canis lupus*). With the end of licensed hunting (and minimal subsistence hunting), I would expect that caribou populations should increase unless they are severely limited by food shortage or predation.

Seasonal food shortages have been shown to affect caribou reproduction and recruitment in a variety of ways (*e.g.*, Thomas 1982; Cameron *et al.* 1993), and can be examined through the study of reproductive events. Predation may be facilitated by logging and other changes to habitat that favour early seral stage forests. Young forest stands are thought to support increased densities of moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) that in turn support increased densities of wolves (*e.g.*, Schwartz and Franzmann 1989). The preference of wolves for caribou and other small ungulates (Holleman and Stephenson 1981) means that the presence of moose may exacerbate predation on woodland caribou (Bergerud and Ballard 1988).

The objectives of this study were to delineate caribou populations in the region, to compare their demographic parameters, and to identify their limiting factors. Specifically I sought to test the null hypotheses that there were no differences in rates of adult survival, pregnancy, recruitment, or population increase; either among years, populations, or ecoregions. More generally I tested the null hypothesis that there was no change in the number of woodland caribou in the study area.

3.2 Methods

3.2.1 Study Area

The study area (Fig. 3.1) lies between approximately 53°30'N to 56°00'N and 103°30'W to 110°00'W. Although mostly within the Mid-Boreal Upland ecoregion, this area also includes adjacent portions of the Mid-Boreal Lowland and portions of the Churchill River Upland south of the Churchill River (Ecological Stratification Working Group 1995). Mid-Boreal Upland topography is mainly undulating to rolling plains of glaciolacustrine and glaciofluvial origins. The Mid-Boreal Lowland is a relatively level glaciolacustrine floodplain, and the Churchill River Upland is a rolling Precambrian plain (Harris *et al.* 1989). The climate is cool and subhumid with mean January and July temperatures of -19°C and +16°C, respectively. Mean annual precipitation is 46 cm, including a mean snowfall of 1.5 m

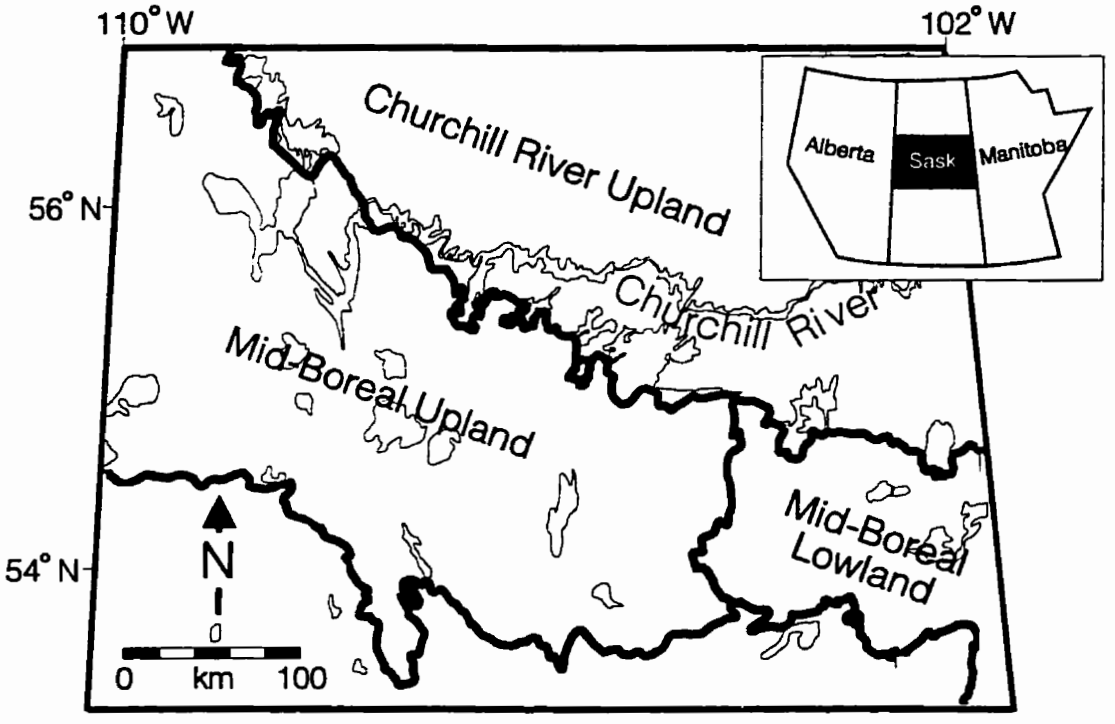

Fig. 3.1 The study area is the Mid-Boreal Upland ecoregion and adjacent portions of the Mid-Boreal Lowland and Churchill River Upland ecoregions within Saskatchewan. Inset shows the location of the larger map in Saskatchewan (Sask).

(Atmospheric Environment Service 1993).

Vegetation in the area is frequently subjected to fire, an integral feature of the boreal forest and its biodiversity (Rowe 1970; Rowe and Scotter 1973). Dominant tree species are white spruce (*Picea glauca*), black spruce (*P. mariana*), jack pine (*Pinus banksiana*), and aspen (*Populus tremuloides*). Other important species are balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), tamarack (*Larix laricina*), and balsam poplar (*Populus balsamifera*). Major upland vegetation communities were described in Chapter 2.

The distribution of woodland caribou in the study area is highly heterogeneous in response to habitat characteristics, and Ruttan (1960) observed few interactions among individual caribou groups in the region. Other ungulates in the area include moose, white-tailed deer, and elk (*Cervus elaphus*). Although wolves have been observed preying upon caribou in the region, moose and white-tailed deer are likely more common prey items (Ruttan 1960; Trottier 1986). In addition to wolves, other large carnivores include coyotes (*Canis latrans*), black bears (*Ursus americanus*), and lynx (*Lynx canadensis*).

3.2.2 Capture

Caribou were captured either by darting (n = 37), or by net-gunning (n = 25). Forty-three different adult

females were captured between March 1992 and January 1995. Forty of the females were fitted with coloured ear tags and radio-collars equipped with both satellite and VHF transmitters. Four animals were killed during the study, three from physical injuries sustained during darting and one from capture myopathy when she was darted after a prolonged pursuit following partial capture with a net. All captures occurred in winter between 13 December and 14 March. I extracted a tooth for aging and blood samples for pregnancy testing from most animals at the time of capture. Total body length, girth, mandible, and metatarsal measurements were made to the nearest 5 mm following the methods of Dauphiné (1976). Animal capture and handling procedures followed University of Saskatchewan animal care protocol 920092.

3.2.3 Population delineation

Animal locations were obtained from satellite transmitters that were programmed to transmit for 8-h periods every 4th day from 1 August to 30 April, and every 2nd day from 1 May to 31 July. Keating *et al.* (1991) found that the accuracy of locations from satellite telemetry systems was greatly dependent upon the correct elevation being specified for each transmitter. I specified the elevation at the transmitter deployment site as that to be used in the calculations of locations. One location of

quality class 1 or higher (Service Argos 1988) was selected for each animal for each transmission period. Selection was based first on location quality and then on the number of signals received during the satellite overpass. Locations were examined for outliers by calculating the ξ-value described by Keating (1994). Keating's ξ-value is calculated from consecutive movement vectors and identifies out-and-back movements indicative of erroneous locations. When $\xi \leq 5$ km, the location was retained. When $5 \text{ km} < \xi \leq 10$ km, the location was deleted only if it was contradicted by the other locations obtained during the same transmission period. For any $\xi > 10$ km, I deleted the location unless it was confirmed by a second location during the same transmission period. Deleted locations were replaced by the next best location from the transmission period (when available), subject to the same selection and outlier screening criteria. A total of 71 locations were replaced and 12 were deleted without replacement, yielding 7299 locations for the 40 radio-tracked animals.

Locations were used to calculate 100% minimum convex polygons for each animal using the computer program HOME RANGE (Ackerman *et al.* 1990). The minimum convex polygons were plotted and the degree of overlap among polygons was used to subjectively establish membership in distinct

populations within the regional metapopulation (sensu Wells and Richmond 1995).

3.2.4 Survival

Satellite transmitters were each equipped with 24-h activity sensors, which enabled us to determine exact dates of mortality. Mortality sites were typically inspected several weeks after death ($\bar{x}$ = 54 days, n = 8, range = 17 - 152 days). Cause of death was attributed to predation when the remains were disarticulated and crushed (Hearn *et al.* 1990).

Seasonal survival rates and 95% confidence intervals were calculated independently for each population and for the metapopulation using the Mayfield (1975) method in the computer program MICROMORT (Heisey and Fuller 1985). Five seasons were determined from calving dates, snow cover, and plant phenology: post-calving (16 May - 30 June); summer (1 July - 15 September); autumn (16 September - 30 November); early winter (1 December - 28 February); and late winter - spring (1 March - 15 May). Data from animals with transmitters that failed and for which fate was unknown were included to the end of the last complete season of data collection. Within MICROMORT, seasonal survival rates were calculated from the number of radio-tracking days (n = 23 222) and the number of mortalities occurring during each

season. Annual survival rates and variances were calculated from seasonal survival rates within MICROMORT.

3.2.5 Age and pregnancy determination

Ages were determined by counting tooth cementum annuli (Miller 1974). Pregnancy was determined using serum progesterone levels with reference to levels in animals with known reproductive status (calf or fetus observed (n = 34), this study). Progesterone levels for individuals whose pregnancy status was unconfirmed (n = 17) were tested using a one-tailed comparison of a single sample with a sample mean (Sokal and Rohlf 1981 p. 231, α = 0.05, df = 33) and overall pregnancy rates determined. Progesterone levels were also compared with those presented in Figure 1 of Rehbinder *et al.* (1981) who reported annual maximum progesterone levels in non-pregnant captive reindeer of about 0.4 ng mL^{-1}, and minimum levels in pregnant animals (between 20 and 200 days post conception) of about 1.3 ng mL^{-1}. The standard deviation for the overall pregnancy rate was calculated from the binomial distribution (Sokal and Rohlf 1981).

3.2.6 Parturition, recruitment, and group size

Aerial surveys to determine rates of parturition and group composition were conducted between March 1992 and March 1996. Flights provided a single observation of each

collared cow in each survey period. Surveys during the rut occurred between 28 September and 3 October, late winter surveys during the first two weeks of March, post-calving surveys in late May (14 - 25 May in 1992 and 23 - 25 May in 1993 and 1994), and summer surveys in July and August (1993 and 1994 only). Surveys were conducted from fixed-wing aircraft in 1992 and from helicopters in 1993-1996. Additional data on group composition were obtained during winter capture operations in December 1993, January (1994 and 1995), and February (1993 and 1994). Animals were classified as calves or adults (≥12 months old) based on body size. Adults were further classified to sex either by presence or absence of a vulva patch, or by general morphology (only to identify mature bulls during the rut). Information on group composition was used only when the total group size was reliably determined. I used survey data from all years and all populations to calculate typical group sizes according to the weighted average method of Jarman (1982). For the purpose of calculating calf:cow ratios, I added the requirement that all animals be clearly identified as either adults or calves. Adults of undetermined sex were apportioned according to sex ratios of identified adults within their population in the respective survey period. Unsexed adults constituted 10% (range = 0 - 27%) of all adults in the sample. I used actual calf counts and adjusted numbers of cows to

calculate calf:cow ratios in late winter for each population in each year.

Bergerud (1980) stated that 11 - 12 months was the appropriate age at which to calculate recruitment in caribou, as animals of that age were subjected to sources of mortality at the same rates as older animals. Gauthier and Theberge (1985) also defined recruitment as survival to 1 year, while Fuller and Keith (1981) assumed that calf survival equalled adult survival from February to May, and defined recruitment as survival to 9 months. I considered my March calf:cow ratios to be measures of recruitment. I used the Friedman test in SPSS for Windows (SPSS 1993) to test the hypothesis that recruitment did not differ among years. Standard deviations for the overall parturition rate and for recruitment rates of each population were calculated from the binomial distribution (Sokal and Rohlf 1981).

3.2.7 Rates of increase

Following the method employed by Hearn *et al.* (1990), I used my survival rates and recruitment rates to calculate Caughley's (1977) survival-fecundity rate of increase, r_s. Ratios of males:females among calves reported in caribou studies range from near 0.5:1 (Bergerud 1971; Stuart-Smith *et al.* 1997) to 1.2:1 (Bergerud 1980), with the sex ratio being affected by the population age structure (Thomas *et*

al. 1989). The calculations I employed included the assumption that the sex ratio among 10 month old calves is 1:1.

I used Monte Carlo simulations to produce estimates of survival and recruitment. The estimates were based on the mean values and standard deviations that I had previously determined for each population (based on data pooled over 3 years). Survival estimates > 1.0 were assumed equal to 1.0. I produced 1000 estimates of each variable for each population and used them to determine means and variances of the population rates of increase. The same procedure was employed to calculate a metapopulation mean rate of increase and variance.

A grand mean rate of increase was calculated for all populations (k = 5), using each population mean rate of increase weighted by its precision, according to the following formula:

$$\bar{r}_s = \left(\sum_{i=1}^{k}(\bar{r}_{s_i}/s_i^2)\right) / \left(\sum_{i=1}^{k}(1/s_i^2)\right) \qquad (3.1)$$

where $\bar{r}_s$ is the grand mean rate of increase, and $\bar{r}_{s_i}$ and s_i^2 are the rate of increase and variance, respectively, of population i. The null hypothesis that the population means were the same was then tested using a weighted sum of squares calculated from the grand mean and the population means and variances according to the following formula:

$$X^2 = \sum_{i=1}^{k}((1/s_i^2)\times(\bar{r}_{s_i} - \bar{\bar{r}}_s)^2) \qquad (3.2)$$

where X^2 is the weighted sum of squares which should approximate the chi-square distribution with k-1 degrees of freedom.

3.3 Results

3.3.1 Population Delineation

When I plotted 100% minimum convex polygons calculated from locations of the 40 study animals, I observed that 36 of 40 animals were distributed among 5 populations (Fig. 3.2), while the other four belonged to two different populations. For the remainder of this paper I will refer to five populations (containing a total of 36 radio-collared individuals), and a regional metapopulation (combining data from all 40 animals). Three of the populations (Clarke Lake n = 7 collared animals, Weyakwin Lake n = 6, and Montreal Lake n = 10) restricted their movements to the Mid-Boreal Upland. The range of the Nemeiben Lake population (n = 8) included portions of the Mid-Boreal Upland and Churchill River Upland, while the Mossy River population (n = 5) used both the Mid-Boreal Upland and Mid-Boreal Lowland ecoregions.

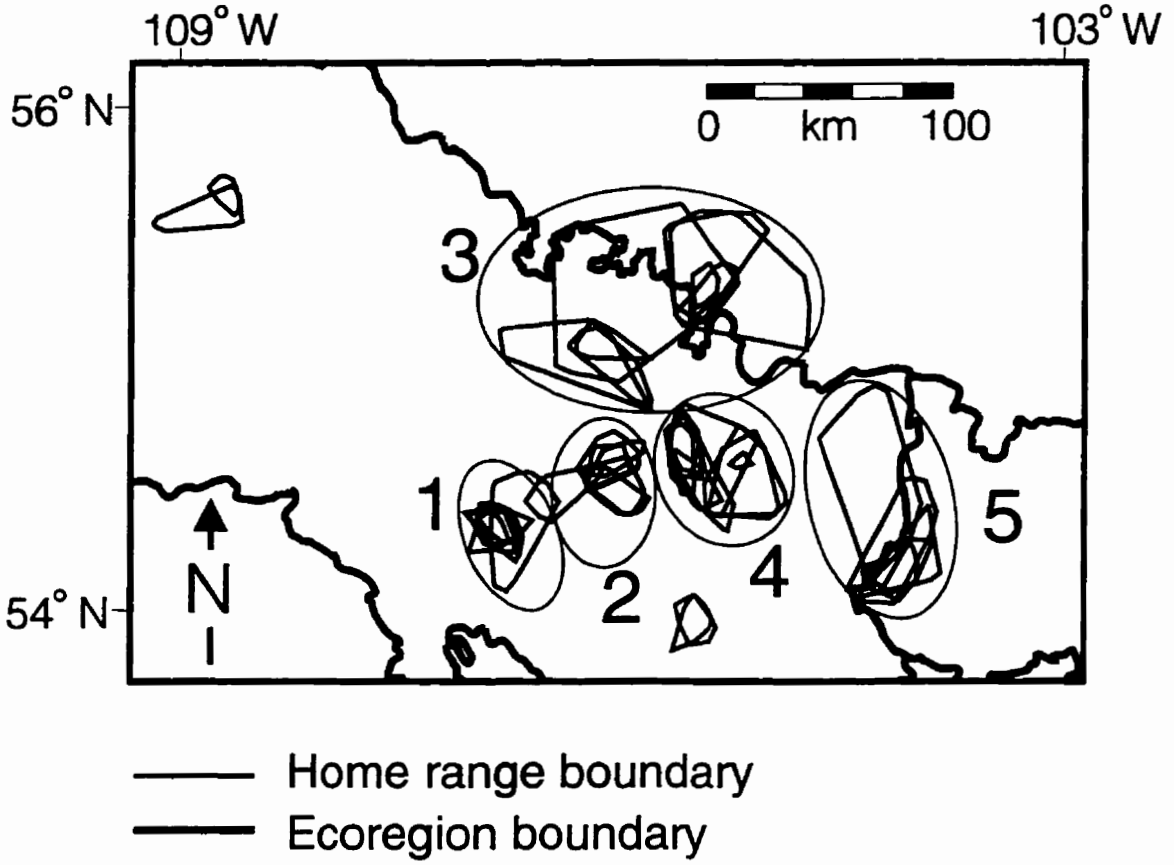

Fig. 3.2 Locations of five study populations as indicated by ellipses around the 100% minimum convex polygons of their members. They are: 1 - Clarke Lake, 2 - Weyakwin Lake, 3 - Nemeiben Lake, 4 - Montreal Lake, and 5 - Mossy River.

3.3.2 Survival

I calculated annual survival rates using data pooled from all years for each population and for the metapopulation (Table 3.1). Data were too limited to conduct meaningful tests for differences among years. I was unable to reject the hypothesis that annual survival rates were the same among the five populations (G = 3.7, df = 4, P > 0.25). To test the hypothesis that survival rates did not differ among the ecoregions, I compared data pooled from the three populations restricted to the Mid-Boreal Upland with the other two populations and did not reject H_0 (G = 3.4, df = 2, P > 0.10).

3.3.3 Timing and Causes of Mortality

Most mortality (8 of 12 cases) occurred during July and August. Of the eight mortality sites visited, three deaths were attributed to wolf predation (all occurred between 31 July and 13 August), three were attributed to unknown predators (mortality dates: 1 May, 27 July, and 1 November), and two were attributed to causes other than predation (12 July and 23 August). Four sites were not visited for technical reasons (3 VHF transmitter failures and one mortality at the end of the study).

Table 3.1 Annual survival rates of adult female woodland caribou in Saskatchewan, by population and year.

Population†	1993-94	1994-95	1995-96	1993-96*	95% CI*
Clarke Lake	1.00 (4.8)	0.57 (4.6)	1.00 (4.0)	0.80 (13.4)	0.62 - 1.00
Weyakwin Lake	---	1.00 (3.2)	0.82 (5.2)	0.87 (9.2)	0.66 - 1.00
Nemeiben Lake	---	0.79 (5.1)	0.72 (6.2)	0.79 (12.3)	0.60 - 1.00
Montreal Lake	1.00 (5.0)	0.50 (4.7)	1.00 (3.0)	0.78 (12.9)	0.60 - 1.00
Mossy River	---	1.00 (2.9)	1.00 (5.0)	1.00 (8.6)	1.00 - 1.00
Metapopulation*	1.00 (13.3)	0.71 (23.8)	0.89 (26.4)	0.84 (63.6)	0.75 - 0.93

* Calculations based on pooled data.

† See Fig. 3.2 for locations.

() numbers in parentheses represent the number of animal-years of data. Metapopulation totals include data from populations other than the five listed.

--- no data.

3.3.4 Pregnancy and parturition

The mean and standard deviation of serum progesterone levels calculated for cows whose pregnancies were confirmed by observation of a calf or fetus (n = 34) was 5.8 ± 2.6 ng mL^{-1}. When I failed to observe an individual cow with a calf or fetus I used her serum progesterone level at the time of capture to determine pregnancy (n = 17). Animals with progesterone levels > 1.3 ng mL^{-1} were considered pregnant (n = 14), while those with lower progesterone levels were categorized as non-pregnant (n = 3). All three non-pregnant animals had progesterone levels < 0.3 ng mL^{-1}, while the 14 animals determined to be pregnant had levels ≥ 2.4 ng mL^{-1}. I was not able to detect a difference in pregnancy rates among yearlings and adult cows with and without a calf at heel during the rut (Table 3.2, G = 0.18, df = 2, P > 0.90). No differences among years or populations were apparent. The overall pregnancy rate was 94 ± 3%.

For 1994-1996, the minimum parturition rate among 28 pregnant cows was 86 ± 7%. The earliest date on which I observed a calf was 14 May, although I received reports of un-collared cows with calves as early as 7 May. Had I only considered data from May surveys, I would have concluded that the minimum parturition rate was 79 ± 8% (n = 22 of 28) as the remaining (n = 2) calves were observed on subsequent surveys.

Table 3.2 Pregnancy rates of woodland caribou from Saskatchewan in 1992-1995, as determined from serum progesterone levels.

Status in autumn	Pregnancy	(*n*)
Yearling (16 months)	1.00	(5)
Cow (≥28 months) with calf	0.85	(13)
Cow (≥28 months) without calf	0.97	(33)
Total	0.94	(51)

3.3.5 Recruitment

There was no detectable difference in calf recruitment to 10 months among years (Friedman test, Fr = 0.1, n = 5, k = 3, P = 0.95) so I pooled data from 1994-1996 (Table 3.3). I could not reject H_0 that there were no differences in March calf:cow ratios based on pooled data for the 5 populations (G = 3.1, df = 4, P > 0.50). When I tested for differences in recruitment among ecoregions for the 1994-1996 period I also failed to reject the H_0 of no differences (G = 2.9, df = 2, P > 0.10).

3.3.6 Group Size

The typical group size (Table 3.4) of 2.0 animals that I observed on my May surveys mostly consisted of cow-calf pairs. On only four occasions did I observe two adult animals together in May. The summer group size of 1.3 was the annual minimum and groups consisted exclusively of solitary cows or a cow plus a calf. Typical group sizes increased up to and following the rut, peaking in early winter at 8.2 animals. On two occasions calves were observed accompanying cows during the rut, when the same cows had been observed without calves on previous surveys. The typical group sizes reported for May, July, and August surveys should therefore be regarded as minimal values for those periods.

Table 3.3 March* calf:cow ratios among different populations of woodland caribou in Saskatchewan, 1994-1996.

Population†	1994	1995	1996	1994 - 96‡
Clarke Lake	0.23 (26)	0.55 (11)	0.37 (11)	0.33 (49)
Weyakwin Lake	0.11 (9)	0.29 (17)	0.56 (9)	0.31 (35)
Nemeiben Lake	0.10 (10)	0.08 (25)	0.35 (20)	0.18 (55)
Montreal Lake	0.39 (13)	0.39 (13)	0.30 (10)	0.37 (35)
Mossy River	0.27 (8)	0.24 (21)	0.20 (10)	0.24 (38)
Metapopulation‡	0.24 (74)	0.24 (89)	0.35 (60)	0.28 (223)

* For 1994 the following exceptions were noted for dates of data collection: Clarke Lake, 11 February to 15 March 1994; Weyakwin Lake, 18-19 December 1993; Mossy River, 21-23 January 1994.

† See Fig. 3.2 for locations.

‡ Calculations based on pooled data.

() numbers in parentheses represent the adjusted numbers of cows, where adjusted number of cows = cows observed + (cows observed / total adults observed and sexed) x unsexed adults observed. Totals across years may not add up owing to the existence of fractional numbers of cows arising from the calculation of adjusted numbers. Metapopulation totals include data from populations other than the five listed.

Table 3.4 Typical sizes of groups of caribou observed in Saskatchewan in different months; data pooled across all years and populations.

Month	TGS	SE	Range	*n*	*m*
May	2.0	0.4	1 - 3	86	46
July / Aug.	1.3	0.5	1 - 2	20	17
Sept./ Oct.	3.9	1.9	1 - 7	177	60
December	8.2	4.5	2 - 16	109	18
January	5.5	3.2	1 - 12	96	26
February	7.0	5.0	1 - 18	137	31
March	5.7	2.7	1 - 13	435	101

n numbers of individuals observed

m numbers of groups observed

TGS Typical group size $= \sum_{i=1}^{m} n_i^2 / \sum_{i=1}^{m} n_i$ where n_i is the number of individuals in group i.

SE standard error (TGS) $= \left(\left[\sum_{i=1}^{m} n_i^3 - \left(\sum_{i=1}^{m} n_i^2 \right)^2 / \sum_{i=1}^{m} n_i \right] / \left(\sum_{i=1}^{m} n_i - 1 \right) \right)^{0.5}$

Calculations after Jarman 1982, p. 336.

3.3.7 Rates of increase

I employed recruitment and survival rates for each population and for the metapopulation to determine population rates of increase (Table 3.5). I did not reject the hypothesis that the individual populations had the same rates of increase during the study (X^2 = 7.37, df = 4, P > 0.10) or the hypothesis that the metapopulation was stable during the study period (Z = 0.83, P = 0.20). I also tested the null hypothesis that there was no difference in rates of increase among ecoregions (Mid-Boreal Upland, Mid-Boreal Lowland, and Churchill River Upland) and found evidence for its rejection (X^2 = 6.66, df = 2, P < 0.05).

3.4 Discussion

The apparent fragmentation of the caribou metapopulation in central Saskatchewan into relatively discrete populations supports Ruttan's (1960) observations of limited interactions among groups of caribou, and is consistent with recent observations in Québec (Ouellet *et al.* 1996) and Alberta (Stuart-Smith *et al.* 1997). Furthermore, road building and forestry activity subsequent to Ruttan's report have placed potential barriers between adjacent groups. Despite this spatial segregation, I did not find significant differences among individual populations in survival or recruitment rates, or in rates

Table 3.5 Annual rates of increase ($\bar{r}_{s_i}$) of woodland caribou populations in Saskatchewan for 1993-1996.

Population[†]	Calf:cow	Survival	$\bar{r}_{s_i}$[*]	sd[*]
Clarke Lake	0.33	0.80	-0.08	0.14
Weyakwin Lake	0.31	0.87	-0.02	0.14
Nemeiben Lake	0.18	0.79	-0.16	0.15
Montreal Lake	0.37	0.78	-0.09	0.14
Mossy River	0.24	1.00	0.11	0.03
Metapopulation[‡]	0.28	0.84	-0.05	0.06

* $\bar{r}_{s_i}$ and standard deviations calculated from 1000 r_{s_i} values for each population using calf:cow ratios and survival rates generated by Monte Carlo simulations, where

r_{s_i} = ln(female survival + female survival × calf:cow × 0.5), and assuming a 1:1 calf sex ratio.

† See Fig. 3.2 for locations.

‡ Calculations based on pooled data.

of increase. Trends in the data, however, suggest that the Nemeiben Lake population, inhabiting portions of the Precambrian shield in the northern part of the study area, has a lower rate of increase than the populations to the south. The high positive rate of increase for the Mossy River population is largely attributable to none of the radio-collared animals in this area dying during the study, providing me with a spurious estimate of 100% survival with no variation. A lack of variation in the survival estimate resulted in low variance around the $\bar{r}_{s_i}$ value for the Mossy River population, which was then given disproportionate weight in the calculation of $\bar{\bar{r}}_s$ (using Equation [3.1]). This anomaly affected comparisons of $\bar{r}_{s_i}$ values among populations and among ecoregions and produced a significant result in the comparison of rates of increase for the three ecoregions. I therefore believe that there is insufficient evidence to conclude that there are significant differences in rates of increase among ecoregions. Any significant differences among rates of increase for different populations would have necessitated knowledge of relative population sizes to calculate the rate of increase for the metapopulation. Overall, my results suggest that the caribou metapopulation in central Saskatchewan is relatively stable. I recommend caution in evaluating these results as I have data for only 3 years, and long-term trends may be somewhat different.

Rock (1992) believed that the decline in the regional caribou population in the early 1970s could be largely attributed to hunting pressure and Trottier (1988) reported that some local herds were eliminated by hunting. If over-hunting was solely responsible for the population decline then I would expect the moratorium on licensed hunting, in place since 1987, and low levels of subsistence hunting (Trottier 1986) to result in an increase in the metapopulation. The lack of population growth reported here suggests that other factors must be involved in reducing adult survival and/or limiting recruitment.

3.4.1 Adult survival

The annual survival rate for adults of 0.84 observed in this study is consistent with those reported for other populations of woodland caribou (0.85 in Alberta, Fuller and Keith 1981; 0.75 in Alberta, Edmonds 1988; 0.71 - 0.92 in British Columbia, Seip 1992; 0.88 in Alberta, Stuart-Smith *et al.* 1997). A 16% adult mortality rate is not inconsistent with increasing caribou populations (*e.g.*, Fancy *et al.* 1994), although it is higher than the 5%-13% range of natural adult mortality reported by Bergerud (1983). Death was attributed to predation at 75% of the mortality sites investigated. The mortality rate of adult caribou may not, by itself, be sufficient to explain the

lack of increase in the caribou populations in central Saskatchewan.

3.4.2 Food limitation and recruitment

Many studies have shown food limitation to have direct effects on life history events of cervids, especially reproduction. Poor nutrition is associated with delayed reproductive maturity (Thomas 1982; Skogland 1986; Messier *et al.* 1988; Crête and Huot 1993), and conception by yearling caribou cows occurs only when nutrition is especially good (Bergerud 1980; Parker 1981). Parker (1981) reported that pregnant 22-month-old cows were significantly larger and heavier than non-pregnant individuals of the same age. I observed that 100% of yearlings were pregnant in my study area.

Poor nutrition is also related to suppressed or delayed ovulation within a given year (Cameron *et al.* 1993). In general, lower pregnancy in cervids is related to poor body condition at the rut (Dauphiné 1976; Messier *et al.* 1988; Cameron 1994) due to poor summer nutrition (Thomas 1982; Crête and Huot 1993; Cameron and ver Hoef 1994). Cameron (1994) explained that the inability to compensate for the costs of gestation and lactation will eventually result in a reproductive pause, though early loss of a calf may permit a female to avoid the costs of lactation and recover from the costs of gestation prior to

the next breeding season. Like Seip (1992), I did not find a difference in pregnancy rates between those cows that had successfully reared a calf through the summer, and those that had not. The overall pregnancy rate that I observed, 94% of adult females, was identical to that reported from British Columbia by Seip (1992) and higher than the mean of 82% reported for caribou throughout North America (Bergerud 1980), though both Bergerud (1980) and Seip (1992) excluded yearlings in their calculations. I interpret the high pregnancy rate in my study to be indicative of adequate summer nutrition.

While poor summer nutrition is related to lower rates of pregnancy, poor nutrition in winter may result in abortion in extreme cases (Gates *et al.* 1986), or in low birth weight calves and late parturition dates (Skogland 1983; Couturier *et al.* 1990; Cameron *et al.* 1993). Timing of parturition has been suggested to be delayed until fetal size is sufficient for survival (Skogland 1983; Cameron *et al.* 1993), while early birth is advantageous as it permits maximum growth prior to insect season as well as before the following winter (Skogland 1983). Conversely, delayed birth is associated with higher calf mortality (Skogland 1986; Couturier *et al.* 1990; Cameron *et al.* 1993). The 86% minimum parturition rate that I report, along with a mean calving date of 15 May (unpublished data) indicates that winter nutrition is also adequate. In my study, early

reproductive maturity, large adult body size (unpublished data), high pregnancy rate, high parturition rate and early calving all point to good maternal condition throughout the year, and suggest that calves should be in excellent physical condition.

3.4.3 Predation and recruitment

Calf mortality has been viewed as a major factor limiting population growth in many caribou herds (Dauphiné 1976; Van Ballenberghe 1985; Adams *et al.* 1995). Bergerud (1983) has theorized that predation on calves can prevent population increase or cause population decline, but the relative importance of different mortality agents is often unknown (Whitten *et al.* 1992; Adams *et al.* 1995). For the reasons I have outlined above, low calf survival is not likely related to neonatal condition, and inadequate nutrition is not likely to be the factor limiting population growth of caribou in my study. With regard to maternal behaviour, my survey data show that caribou cows in the study populations were typical in their tendency to space out and calve alone, as has been observed elsewhere (Fuller and Keith 1981; Brown and Theberge 1985; Edmonds 1988). Observations indicate that the decline from the typical group size of 2.0 at calving to 1.3 in mid summer represents neonatal mortality and/or missed observations due to dense foliage or avoidance of observers as reported

in Newfoundland (Chubbs 1993). Although summer survey data underestimate calf survival, they suggest that most calf mortality occurs during the first 4-6 weeks of life, in agreement with the findings of Fuller and Keith (1981) and Stuart-Smith *et al.* (1997). I agree with Bergerud (1983) and Bergerud and Elliot (1986) that predation is the most likely explanation for high calf mortality, as recently reported by Adams *et al.* (1995). Predation on adults and calves appears to be the proximate factor limiting the increase of caribou populations in central Saskatchewan.

3.4.4 Habitat alteration and predation

Habitat alteration through road building and logging provides an increase in the abundance of forest stands in early seral stages, which may promote an increase in moose and white-tailed deer populations. Prevailing theory suggests that an increase in the abundance of alternate prey facilitates an increase in wolf density (Bergerud and Ballard 1988). Based on the minimum moose density (0.2 moose$\cdot$km^{-2}) that Messier (1985) calculated as necessary to support a wolf population, it is improbable that the caribou density in my study area (<0.05 caribou$\cdot$km^{-2}) is sufficiently high to support wolves in the absence of other ungulate prey. The same increase in early seral stage forests may also result in higher densities of black bears (Schwartz and Franzmann 1991).

In several recent studies, bear predation has been shown to be, or thought to be, the most important source of predation on both moose calves (Hauge and Keith 1981; Ballard *et al.* 1991) and caribou calves (Adams *et al.* 1995). Seip (1992) dismissed wolf predation as the major cause of early calf mortality because he observed similar mortality rates in areas with and without wolves, though other predators were present in both areas. Adams *et al.* (1995) noted that the distribution of grizzly bears (*Ursus arctos*) at the time of caribou calving may result in a greater likelihood of caribou calves being discovered by bears than wolves. Caribou may actually select calving sites to minimize contact with wolves as suggested by Bergerud and Elliot (1986), Bergerud and Ballard (1988) and Adams *et al.* (1995). Such a strategy may not allow caribou to simultaneously minimize contact with black bears.

The findings of Schwartz and Franzmann (1991) show the spring diet of black bears to consist primarily of bog cranberry (*Vaccinium vitis-idaea*), horsetails (*Equisetum* spp.), grasses, and sedges. Paré and Huot (1985) reported horsetails and graminoids to be important items in the spring diet of caribou in the Caniapiscau herd, and in my study area Thomas and Armbruster (1996) also showed that woodland caribou make extensive use of horsetails and sedges in their spring diet. The treed peatlands and adjacent black spruce stands that are used extensively for

calving have the highest abundance of sedges and bog cranberry of any habitat types available (Chapter 2). Though I lack data on causes of calf mortality, it is possible that caribou cows are sharing their calving range with black bears at a time when calves are vulnerable to bear predation. Because bears are not obligate carnivores their densities may be independent of ungulate density.

The high natural mortality rate among adults, however, cannot be explained by bear predation, and predation on adult animals by wolves may ultimately be the most influential factor in limiting the populations' rates of increase. Fancy *et al.* (1994) modelled the rate of growth in the Porcupine caribou herd and determined that it was approximately three times more sensitive to a change in adult female survival rate than to a change (of the same magnitude) in recruitment rate. To maintain a given population, a slight but persistent increase in adult mortality requires a threefold, and equally persistent, increase in recruitment. While adult survival rates in large mammal populations are relatively stable (Fowler 1981), calf survival in caribou can be highly variable among years (Bergerud 1971; Bergerud 1980; Fancy *et al.* 1994).

In this study, the Nemeiben Lake population had the highest rate of decline among the study populations at a time when the area had a low abundance of moose, a

declining white-tailed deer population and high wolf and black bear populations (T. Trottier pers. comm.). Abundant predators and a shortage of alternate prey may have increased predation on caribou calves and adults in the area.

If predation on calves and adults is the proximate limiting factor of the regional caribou population, then the ultimate cause likely relates to long-term habitat alteration. This may operate through increased wolf predation, sustained by an increased abundance of other ungulates in early seral stage forests. Population limitation may also occur through increased predation by black bears, with the bears able to sustain themselves on vegetation in the same early seral stage forests. In either instance, the number of predators is probably independent of caribou density, and Messier (1994) outlined how such density independent mortality agents can shift prey densities to lower equilibrium points.

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4. HIERARCHICAL HABITAT SELECTION BY WOODLAND CARIBOU: ITS RELATIONSHIP TO LIMITING FACTORS

4.1 Introduction

Habitat selection research begins with habitat description and ends with an estimation of how selection of habitats affects individual fitness. Over time, the process is an iterative one, as environmental features affecting fitness are those best used to define habitat. In addition to defining relevant habitat types, selection studies must carefully consider the scale at which questions are being posed and the scale at which individuals are selectively satisfying their habitat requirements (Johnson 1980). I propose that there should be a direct relationship between the importance of specific factors limiting populations and the level at which individuals exhibit selective behaviour to minimize the effects of those factors. In general, the scale of selection for various resources should reflect the relative importance of each resource for escaping the effects of limiting factors. The spatial and temporal scales at which various resources are selected should match, with decisions over coarse spatial scales being made at broader time

scales and decisions affecting finer spatial scales being made at finer temporal scales. A limiting factor should continue to dominate selective behaviour at successively finer scales until it becomes less important than the next most important limiting factor.

Caribou (*Rangifer tarandus*) is a circumpolar species whose limiting factors have been argued to include predation, disease, snow conditions, insect harassment, and food. It is generally accepted that predation is the proximate factor limiting populations of woodland caribou (*R. t. caribou*) across North America (*e.g.*, Bergerud 1974; Bergerud 1980; Seip 1992; Ouellet *et al.* 1996; Stuart-Smith *et al.* 1997; Chapter 3). Increased predation on caribou has been linked to higher densities of moose (*Alces alces*) that support high density wolf (*Canis lupus*) populations (Bergerud and Ballard 1988). Moose density has been shown to increase with an increase in the level of habitat disturbance from logging (*e.g.*, Forbes and Theberge 1993; Heikkilä and Härkönen 1996; Rempel *et al.* 1997) or burning (*e.g.*, Peek 1974; Schwartz and Franzmann 1989; Rempel *et al.* 1997). The increases in moose density may lag behind disturbance, depending on the proximity of moose available to colonize the area, and on the severity of the disturbance (Gasaway *et al.* 1989; Loranger *et al.* 1991; Rempel *et al.* 1997). In Alaska, peak moose density occurred at about 15 years post-fire, and by 40 years post-

fire the moose densities had declined to pre-burn levels (Schwartz and Franzmann 1989). Ultimately, habitat alteration may be the factor that facilitates increased predation on woodland caribou by providing habitat for other prey species that, in turn, support a higher density of predators (Cumming 1992). In multi-prey systems caribou must become less profitable prey, especially during calving (Bergerud and Page 1987). Owing to the relationships between forest disturbance and increased moose densities, higher wolf numbers, and declines in caribou density I would expect to find caribou avoiding burns, clearcuts, and early seral stage forests.

In central Saskatchewan, I identified predation as the primary factor limiting five woodland caribou populations in the region (Chapter 3). Because the same limiting factors are at work in all populations in the region, and because the vegetation communities were based on data believed to reflect resources important to caribou, I expected that habitat selection patterns should be repeated across all populations. Other studies conducted at similar scales have reported that caribou are thought to select habitat to reduce predation risk (Bergerud *et al.* 1984; Bergerud and Page 1987; Thomas and Armbruster 1996), especially in winter and during calving (Helle 1980; Bergerud *et al.* 1984). For example, caribou are known to

disperse from other ungulates, including other caribou, for calving (Ouellet *et al.* 1996; Stuart-Smith *et al.* 1997).

The objectives of this study were to identify habitat types selected by woodland caribou at what Johnson (1980) described as the second and third orders. I interpreted caribou behaviour in terms of factors that limit the populations. I predicted that woodland caribou should exhibit second order selection towards habitats less likely to contain high densities of predators. At the third order, I expected that habitat selection should reveal increased selection for habitats that meet microclimate and dietary needs. In a statistical sense, my null hypotheses were that, at each scale, all habitat types would have the same selective value.

4.2 Methods

4.2.1 Study Area

The study area (Fig. 4.1) lies south of the Churchill River between 102°40'W and 110°00'W and from 53°30'N to 56°00'N. The majority of the area is within the Mid-Boreal Upland Ecoregion, but it also includes adjacent portions of the Mid-Boreal Lowland and the Churchill River Upland Ecoregions (Ecological Stratification Working Group 1995). The topography of the Mid-Boreal Upland is mainly undulating plains of glaciolacustrine and glaciofluvial origins, whereas the Mid-Boreal Lowland is a relatively

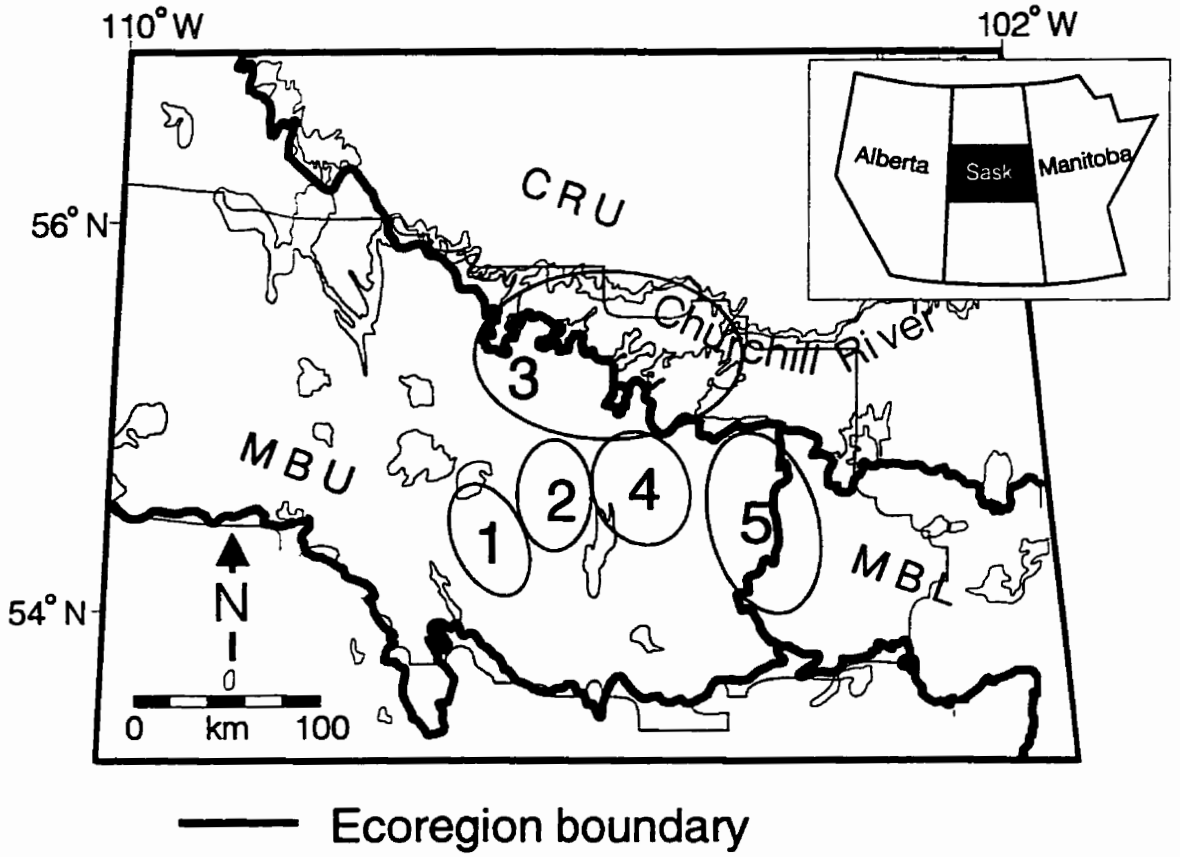


Fig. 4.1 The study area (shaded) is the Mid-Boreal Upland (MBU) ecoregion and adjacent portions of the Mid-Boreal Lowland (MBL) and Churchill River Upland (CRU) ecoregions within Saskatchewan. Inset shows the location of the larger map in Saskatchewan (Sask). Ellipses show the areas inhabited by the 5 study populations (Chapter 3). The populations are: 1 - Clarke Lake, 2 - Weyakwin Lake, 3 - Nemeiben Lake, 4 - Montreal Lake, and 5 - Mossy River.

level glaciolacustrine floodplain, and the Churchill River Upland is a rolling Precambrian plain (Harris *et al.* 1989). The climate is cool and subhumid with mean January and July temperatures of -19°C and +16°C, respectively. Mean annual precipitation in the region is 46 cm, including a mean snowfall of 1.5 m (Atmospheric Environment Service 1993).

Forest stands in the region are dominated by black spruce (*Picea mariana*), white spruce (*P. glauca*), jack pine (*Pinus banksiana*), or trembling aspen (*Populus tremuloides*). Other important tree species include tamarack (*Larix laricina*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and balsam poplar (*Populus balsamifera*). In Chapter 2 I described the major upland vegetation communities in the region as they relate to woodland caribou. Other than caribou, ungulates in the region include moose, white-tailed deer (*Odocoileus virginianus*), and wapiti (*Cervus elaphus*). In addition to wolves, large carnivores include coyotes (*Canis latrans*), black bears (*Ursus americanus*), and lynx (*Lynx canadensis*).

4.2.2 Habitat Delineation

In Chapter 2 I described eight forested vegetation communities available to woodland caribou and indicated that two of them should be combined due to their similarities. I established that there was a high level of correspondence between the seven vegetation communities and

the forest stand attributes in the provincial forest inventory database (Chapter 2). In this paper, I consider these vegetation communities to represent discrete habitat types. Other habitat types considered here include burns, clearcuts, open peatlands, and water (generally open water from 15 May to 15 November and ice covered for the remainder of the year; Masterton *et al.* 1976). The four additional habitat types each appear in the forest inventory database under a distinct code or set of codes. I therefore relied on the provincial forest inventory database for all information pertaining to habitat type. The 11 habitat types appear in Table 4.1.

The Geographic Information System (GIS) attribute databases of the provincial forest inventory and the Prince Albert National Park inventory were used to generate polygons of the 11 habitat types plus an "other" category. Agricultural land appearing in the forest inventory at the forest fringe was deleted. The vector based files were then converted to raster format prior to analyses. The raster size was 31.25 m. Geographic Information System analyses were conducted on Solaris 2.3 and 2.4 based systems; raster based analyses completed in Arc/INFO version 7.0.2 (Environmental Systems Research Institute 1994); and the remaining analyses conducted in Arc/INFO Version 7.0.3 (Environmental Systems Research Institute

Table 4.1 Habitat types available to woodland caribou in the study area in central Saskatchewan.

Description	Habitat code*	Total area (× 1000 ha)	Proportional area	Median patch size (ha)	5% - 95% patch size (ha) range
Jack pine - lichen	JL (A1)	92	0.01	7.4	0.4 - 23.4
Treed peatland	TP (A2)	2498	0.26	23.8	0.3 - 28.4
White spruce	WS (B)	241	0.03	8.0	0.2 - 27.0
Young jack pine	YJ (C)	147	0.02	24.6	0.3 - 80.1
Trembling aspen	TA (D)	1274	0.14	20.1	0.2 - 47.4
Lowland black spruce	LB (E)	79	0.01	6.2	0.4 - 20.8
Upland black spruce - jack pine	UB (F)	2041	0.22	14.3	0.3 - 42.5
Open peatland	OP	317	0.03	5.4	0.1 - 15.2

Water	WA	1313	0.14	37.7	0.1 - 35.8
Clear - cut	CC	83	0.01	21.7	0.3 - 95.5
Burned	B	805	0.09	195.4	0.3 - 61.3
Other	---	543	0.06	6.9	0.2 - 20.1
Total	---	9432	1.00	17.0	0.2 - 32.7

* Habitat codes correspond to those that appear in Figs. 4.2 - 4.4. The labels in parentheses correspond to the vegetation communities described in Chapter 2.

1995).

To account for changes after the most recent revisions in the forest inventory, independent data on logging and forest fires were used to update the existing digital inventory. The database was revised by overwriting existing raster types with burn data up to 1991 and then overwriting the revised database with clearcut data up to 1991. I considered the resulting database to be a description of the area at the beginning of my study in March 1992. Animal locations were overlaid on digital habitat maps chronologically, beginning with March 1992 and updating the habitat database with clearcut and burn information as appropriate. The available data on forest fires and clearcuts were grouped by year rather than by exact date. The burns for each year were added as if they occurred on 15 September, and clearcuts added as if they occurred on 30 November. Clearcuts were always given preference over burns (*i.e.*, when an area was cut and then burned it remained classified as a cut).

The size of each patch of habitat was determined from the rasterized database. A connectivity of eight was specified, which considers rasters to be part of the same patch when they are adjacent or touching corner to corner. Patch sizes were determined following the addition of 1994 fire data, the approximate mid-point of my data collection.

4.2.3 Capture

I captured 40 female caribou between March 1992 and January 1995 and outfitted them with radio-collars equipped with both satellite and VHF transmitters (Chapter 3). Animal capture and handling procedures followed animal care protocol No. 920092 of the University of Saskatchewan.

4.2.4 Reproductive status

I categorized reproductive status to test its effect on habitat selection. Pregnancy was determined from serum progesterone levels (Chapter 3). Aerial surveys to determine parturition rates and group composition were conducted between March 1992 and March 1996 as detailed in Chapter 3. For the purposes of habitat selection analyses, a cow who lost her calf during the year was deemed to have lost it immediately post-partum and was considered to be without a calf for the entire year.

4.2.5 Location data acquisition and preparation

Animal locations were obtained from satellite radio-collar transmitters that were programmed to transmit for 8-hour periods every fourth day from 1 August to 30 April, and every second day from 1 May to 31 July. The elevation at the capture location was specified as that to be used by Service Argos to calculate locations. One location of quality class 1 or higher (Service Argos 1988) was selected

for each animal for each transmission period. Selection was based first on location quality and then on the number of signals received during the satellite overpass. I checked locations for outliers (Chapter 3) and then used the GIS to project latitude and longitude coordinates to Universal Transverse Mercator coordinates. Following screening for outliers I was left with 7299 locations for the 40 radio-tracked animals (Class 1 = 1834, Class 2 = 3219, Class 3 = 2246). Using location data for each animal, I previously determined that 36 of the 40 animals belonged to 5 discrete populations (Chapter 3). The populations appear in Figure 4.1.

4.2.6 Delineation of seasons and calculation of seasonal ranges

I defined five seasons based on calving dates, snow cover, and plant phenology: post-calving (16 May - 30 June); summer (1 July - 15 September); autumn (16 September - 30 November); early winter (1 December - 28 February); and late winter / spring (1 March - 15 May). The years that I refer to in this paper represent "biological years", 12 month periods beginning on 16 May of the year noted (*e.g.*, 1994 data were collected from 16 May 1994 to 15 May 1995).

Locations were used to calculate 100% minimum convex polygons for each animal in each season in which I had more

than 10 locations (n = 324 seasons, median number of points per season = 22, range = 10 - 34) using the computer program HOME RANGE (Ackerman *et al.* 1990). These data were used to describe the general area used by an animal for a given season. The number of seasonal ranges determined for each animal varied (range = 1 to 17 per animal, median = 7.0).

4.2.7 Second order selection analysis

Second order selection analysis (Johnson 1980) was conducted as a Thomas and Taylor (1990) design two study. Analysis was based on Manly *et al.* (1993) considering the study area as available and each seasonal range as the area used by an individual animal. For both availability and use I divided the area of each habitat type by the total study area or seasonal range (respectively) minus the quantity of "other" habitat. The resulting sets of used and available habitat ratios, which always totalled 1.0, were used to calculate a resource selection index for each habitat type, for each animal-season. The resource selection function (the set of b_i's, the standardized resource selection indices; Manly *et al.* 1993, pp. 40-41) for an individual animal in an individual season was considered to be the basic unit of data for my analyses. The GIS was used to determine availability for second order selection analysis after completing updates on cutting and

fires to September 1994, the approximate mid-point of the study. I had data for 216 animal-seasons from 16 May 1994 to 15 May 1996 for caribou in the 5 discrete populations.

4.2.8 Third order selection analysis

Third order selection analysis conformed to the methods of Arthur *et al.* (1996). I determined the radii for measuring availability as the 95th percentile of distances moved over 2- and 4-day intervals (8.0 km and 12.0 km, respectively). When the inter-location interval was 1 day (n = 90) or 3 days (n = 38), I used the 2-day or 4-day radius, respectively, to determine availability. I defined habitat used as the contents of a circle 1.0 km in radius (55th percentile of mean daily movement distances from all data), centred on the telemetry location. For both use and availability, I divided the area of each habitat type within the circle by the total area of the circle minus the quantity of "other" habitat. The resulting sets of used or available habitat ratios totalled 1.00 for each telemetry location. When the inter-location interval exceeded 4 days I deleted the data (n = 483 locations) and I then discarded data from animal-seasons in which I had fewer than 8 locations (n = 121 locations). This screening process left a total of 6695 locations for which I had both use and availability data. The data described 333 animal-seasons, 297 of which were from

caribou in the 5 populations identified. For the 36 caribou in the 5 populations there was a median of 22 locations per season (range = 8 to 34), and a median number of animal-seasons per caribou of 7.0 (range = 1 to 17).

Data were processed with a program written in C** to determine the resource selection probability function (RSPF, the set of H resource selection indices (b_i) where i = 1 to H and H is the number of habitat types) for each animal-season according to formulae in Arthur *et al.* (1996). The RSPF for a single animal-season was considered as the basic datum for subsequent analyses.

4.2.9 Statistical analyses

For both second and third order selection analyses, the 11 habitat-specific selection indices for each animal-season were used to create 10 synthetic variables based on the differences in sequential pairs of b_i values (Arthur *et al.* 1996). I employed the synthetic variables to conduct multivariate analyses of variance (MANOVAs) with the objective of examining the effects of four factors: population, reproductive status, season, and year. For my initial analysis I restricted my data set to the data collected between 16 May 1994 and 15 May 1996 as I had data from all 5 populations only for these two years. In this period I had data from 216 animal-seasons for second order selection analysis and from 225 animal-seasons for third

order selection analysis. Final analyses were conducted separately for each population where the second order analyses included data available from May 1992 to May 1996, while third order analyses employed data from March 1992 to May 1996.

All post-hoc multiple comparisons were conducted using paired *t*-tests on ranks of each habitat type using the Holm's modification of the Bonferroni approach as recommended by Arthur *et al.* (1996). An experimentwise alpha value of 0.05 was used to test for significance in all tests. I use "preferred" and "avoided" as relative terms, and then only when comparing pairs of habitat types for which I detected statistically significant differences by the methods outlined here.

4.3 Results

4.3.1 Habitat types

The 11 habitat types and unclassified areas ("other") are listed in Table 4.1, along with the total areas they occupy, their median patch sizes, and the 5th and 95th percentile patch sizes. Overall, the study area is dominated by treed peatlands and upland black spruce/jack pine stands.

4.3.2 Second order selection

Multivariate analysis of variance indicated that there were significant differences in habitat selection among the five populations, for interactions between population and year and among population, year and reproductive status (Table 4.2). I divided the data by population, added the data from May 1992 to May 1994 for each population and tested for differences related to year using MANOVAs. I did not consider reproductive status within each population as for any given year I typically had sets of 5 seasons of data from each of only 4 or 5 individuals. I detected a significant year effect only for the Clarke Lake Population (Table 4.3).

Mean selection index values and significant differences among habitat types, as determined from multiple comparison tests on ranks of habitat selection indices, are presented for each population in Fig. 4.2a. The general pattern was for animals to prefer the two peatland types (*i.e.*, open peatland and treed peatland) and black spruce stands over all other habitat types. Clearcuts, burns, jack pine-lichen, young jack pine, and trembling aspen stands tended to be selected significantly less than the other habitat types. Water bodies (caribou are known to use shorelines and islands, and also to use ice covered lakes in winter) and white spruce stands were largely intermediate in selection value. They were

Table 4.2 Significance of the effects of various factors on second order habitat selection by five populations of woodland caribou, May 1994 to May 1996, as determined by multivariate analysis of variance. (n = 216 animal-seasons)

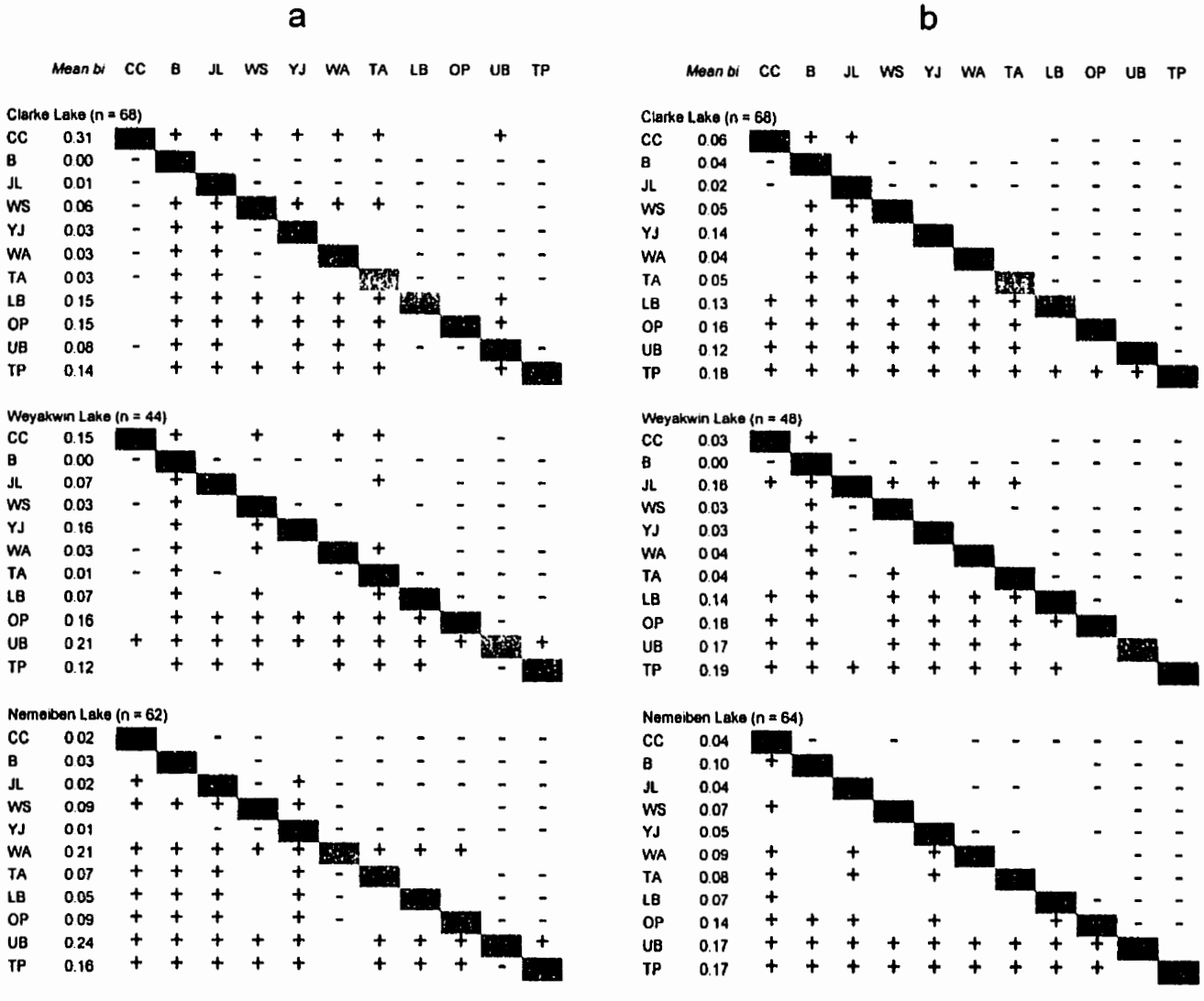
Factor(s)*	Approx. F (Wilks lamda)	df	P
P x R x S x Y	0.41	30, 353	0.998
R x S x Y	0.56	40, 457	0.986
P x S x Y	0.75	160, 1044	0.989
P x R x Y	2.65	40, 457	<0.001
P x R x S	0.59	160, 1044	1.000
S x Y	0.73	40, 457	0.886
R x Y	1.50	10, 120	0.148
R x S	0.33	40, 457	1.000
P x Y	1.52	40, 457	0.025
P x S	0.82	160, 1044	0.948
P x R	0.68	40, 457	0.935
Y	0.82	10, 120	0.609
S	0.89	40, 457	0.671
R	0.88	10, 120	0.558
P	6.57	40, 457	<0.001

* P = Population; R = Reproductive Status; S = Season; and Y = Year.

Table 4.3 Significance of the effect of year on second order habitat selection in individual woodland caribou populations, May 1992 to May 1996, as determined by multivariate analysis of variance.

Population	n^*	Approx. F (Wilks lamda)	df	P
Clarke Lake	68	1.98	30, 162	0.004
Weyakwin Lake	44	1.44	20, 64	0.135
Nemeiben Lake	62	1.42	20, 100	0.129
Montreal Lake	71	1.21	30, 171	0.219
Mossy River	39	0.59	20, 54	0.904

* n = number of animal-seasons.


a
b
Mean bi
CC
B
JL
WS
YJ
WA
TA
LB
OP
UB
TP
Clarke Lake (n = 68)
CC 0.31
B 0.00
JL 0.01
WS 0.06
YJ 0.03
WA 0.03
TA 0.03
LB 0.15
OP 0.15
UB 0.08
TP 0.14
Weyakwin Lake (n = 44)
CC 0.15
B 0.00
JL 0.07
WS 0.03
YJ 0.16
WA 0.03
TA 0.01
LB 0.07
OP 0.16
UB 0.21
TP 0.12
Nemeiben Lake (n = 62)
CC 0.02
B 0.03
JL 0.02
WS 0.09
YJ 0.01
WA 0.21
TA 0.07
LB 0.05
OP 0.09
UB 0.24
TP 0.16
Clarke Lake (n = 68)
CC 0.06
B 0.04
JL 0.02
WS 0.05
YJ 0.14
WA 0.04
TA 0.05
LB 0.13
OP 0.16
UB 0.12
TP 0.18
Weyakwin Lake (n = 48)
CC 0.03
B 0.00
JL 0.16
WS 0.03
YJ 0.03
WA 0.04
TA 0.04
LB 0.14
OP 0.18
UB 0.17
TP 0.19
Nemeiben Lake (n = 64)
CC 0.04
B 0.10
JL 0.04
WS 0.07
YJ 0.05
WA 0.09
TA 0.08
LB 0.07
OP 0.14
UB 0.17
TP 0.17

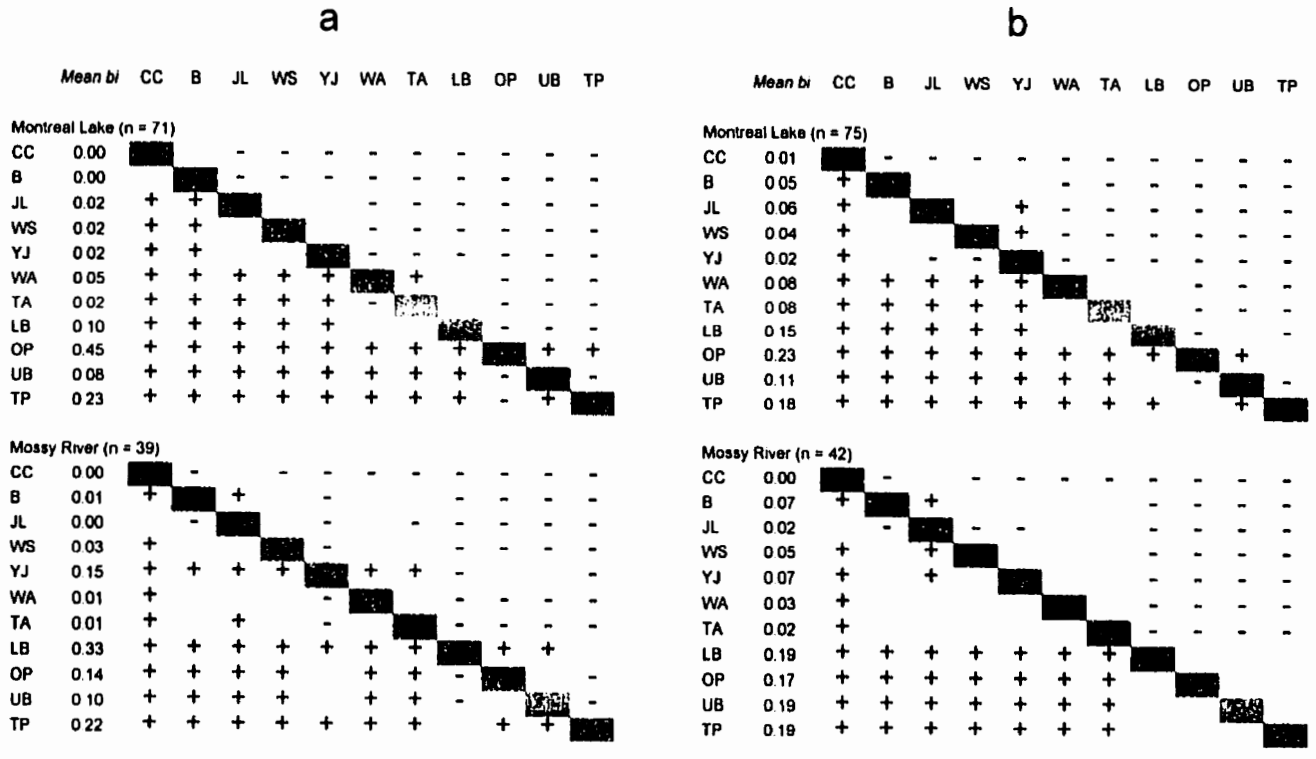


Fig. 4.2 Mean selection indices (b_i) and significant differences between ranks of pairs of the 11 habitat types at: (a) second order selection (May 1992 to May 1996) and (b) third order selection (March 1992 to May 1996) for each woodland caribou population studied. Each row presents the mean selection index value for a habitat type and whether that type was selected significantly more (+) or less (-) than each habitat type listed in the columns. Codes for habitat types appear in Table 4.1.

n = the number of animal-seasons represented by the data.

generally selected significantly less than peatlands and black spruce stands but significantly more than the other types. This pattern was largely consistent across the five populations but there were some local variations. Notable exceptions include the selection of clearcuts by caribou in both the Clarke Lake and Weyakwin Lake populations, and the selection of young jack pine stands by animals in the Mossy River population.

Mean selection indices and significant differences among ranks of habitat types for each year for the Clarke Lake population appear in Fig. 4.3. The pattern appeared to change over the duration of the study in the Clarke Lake area where upland black spruce/jack pine stands and treed peatlands increased in selection value at the expense of clearcuts and open peatlands.

4.3.3 Third order selection

Multivariate analysis of variance indicated that there were significant differences in habitat selection among populations, among seasons, and for interactions between population and reproductive status and between population and season (Table 4.4). I divided the data by population, added the data from March 1992 to May 1994 for each population and tested for differences related to season and reproductive status using MANOVAs. For the Mossy River population I was forced to remove clearcuts as

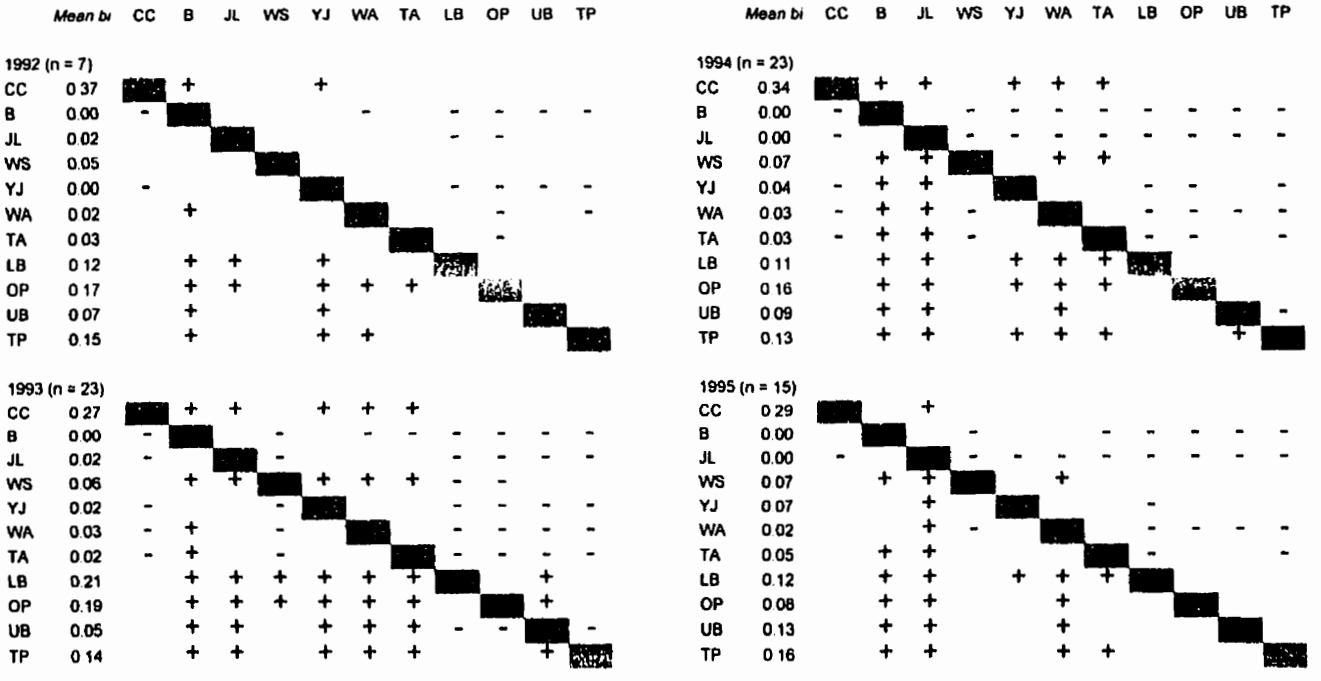


Fig. 4.3 Mean second order selection indices (b_i) and significant differences between ranks of pairs of the 11 habitat types for the Clarke Lake caribou population from 1992 to 1996. Each row presents the mean selection index value for a habitat type and whether that type was selected significantly more (+) or less (-) than each habitat type listed in the columns. Codes for habitat types appear in Table 4.1.

n = the number of animal-seasons represented by the data.

Table 4.4 Significance of the effects of various factors on third order habitat selection by five populations of woodland caribou, May 1994 to May 1996, as determined by multivariate analysis of variance. (n = 225 animal-seasons)

Factor(s)*	Approx. F (Wilks lamda)	df	P
P x R x S x Y	1.07	40, 491	0.366
R x S x Y	1.20	40, 491	0.196
P x S x Y	0.87	160, 1121	0.874
P x R x Y	0.76	40, 491	0.858
P x R x S	1.15	150, 1100	0.115
S x Y	0.90	40, 491	0.651
R x Y	1.37	10, 129	0.203
R x S	1.19	40, 491	0.205
P x Y	0.80	40, 491	0.801
P x S	1.21	160, 1121	0.050
P x R	1.54	40, 491	0.020
Y	0.77	10, 129	0.658
S	1.54	40, 491	0.020
R	1.51	10, 129	0.144
P	2.18	40, 491	<0.001

* P = Population; R = Reproductive Status; S = Season; and Y = Year.

a category when conducting the MANOVA for that population as there was a value of 0.0000 for each animal-season resulting in linear dependence among synthetic variables. Clearcuts were included in the data sets for multiple comparison tests. At the population level I was unable to detect a direct effect of reproductive status or an interactive effect between reproductive status and season on habitat selection for any population. I did detect significant differences in habitat selection among the seasons for the Weyakwin Lake, Nemeiben Lake, and Montreal Lake populations (Table 4.5).

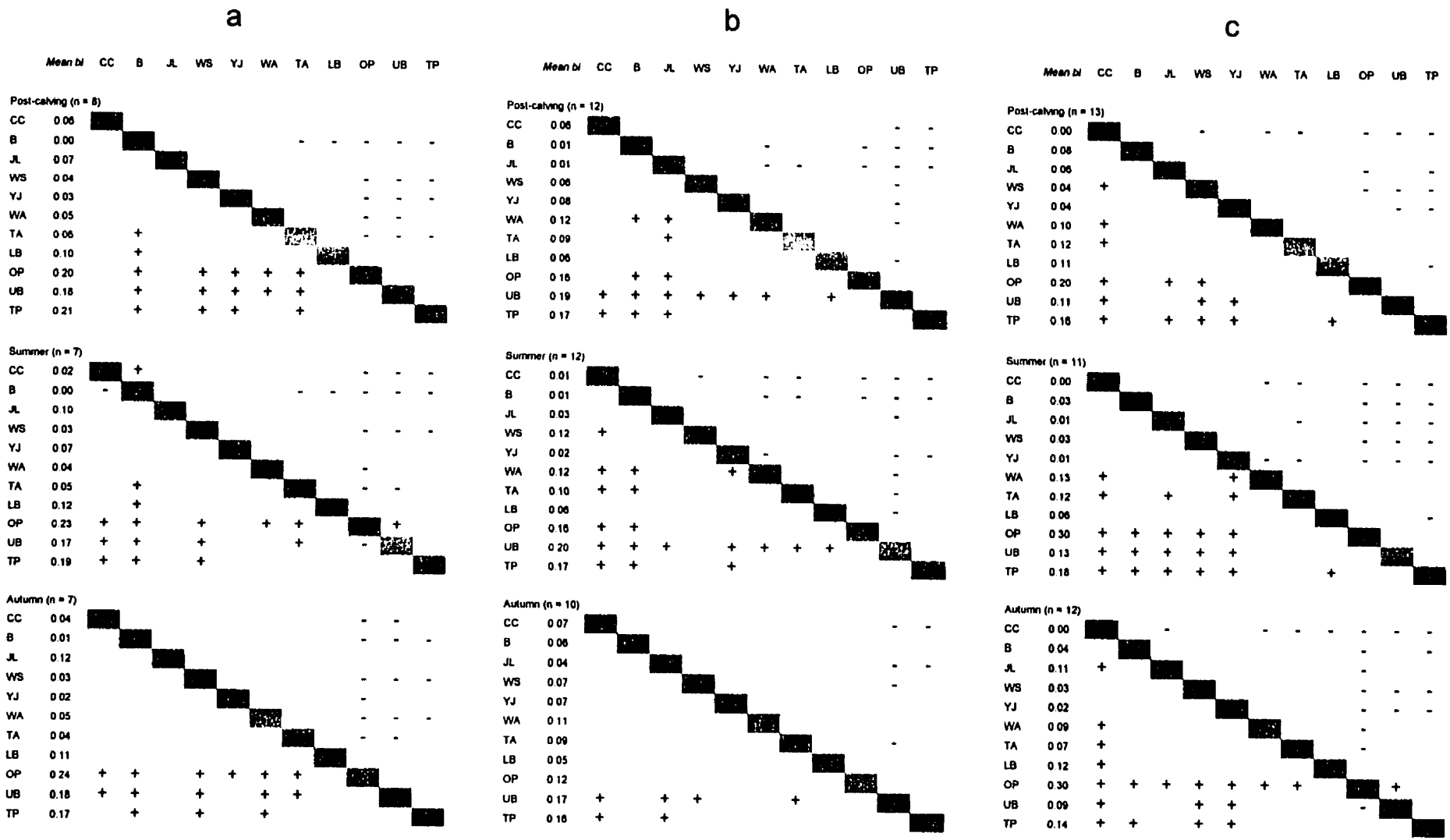
Mean selection indices and significant differences among habitat types, as determined from multiple comparison tests on ranks of habitat selection indices, are presented for each population in Fig. 4.2b. In general, third order selection further focused on the vegetation communities selected at the second order level. Treed peatlands were the most highly selected habitat type, followed by open peatlands, upland black spruce/jack pine forests, and lowland black spruce stands.

Figure 4.4a-c shows mean habitat selection indices and significant differences among habitat types for each season for the Weyakwin Lake, Nemeiben Lake, and Montreal Lake populations. I noted seasonal patterns in the data from these three populations. During the post-calving season, caribou selected upland black spruce/jack pine

Table 4.5 Significance of the effects of season and reproductive status on third order habitat selection in individual woodland caribou populations, March 1992 to May 1996, as determined by multivariate analysis of variance.

Factor(s)*	Approx. *F* (Wilks lamda)	df	*P*
Clarke Lake Population (*n* = 68 animal-seasons)			
R x S	1.24	40, 188	0.172
S	1.24	40, 188	0.176
R	0.89	10, 49	0.550
Weyakwin Lake Population (*n* = 48 animal-seasons)			
R x S	1.03	40, 112	0.434
S	2.05	40, 112	0.002
R	0.80	10, 29	0.631
Nemeiben Lake Population (*n* = 64 animal-seasons)			
R x S	1.09	40, 172	0.339
S	1.50	40, 172	0.040
R	1.16	10, 45	0.340
Montreal Lake Population (*n* = 75 animal-seasons)			
R x S	1.01	40, 214	0.462
S	1.80	40, 214	0.004
R	1.79	10, 56	0.085
Mossy River Population (*n* = 42 animal-seasons)			
R x S	0.57	36, 92	0.971
S	1.15	36, 92	0.296
R	0.50	9, 24	0.861

* R = Reproductive Status; and S = Season.


a
b
c
Mean bl
CC B JL WS YJ WA TA LB OP UB TP
Post-calving (n = 8)
CC 0.06
B 0.00
JL 0.07
WS 0.04
YJ 0.03
WA 0.05
TA 0.06
LB 0.10
OP 0.20
UB 0.16
TP 0.21
Summer (n = 7)
CC 0.02
B 0.00
JL 0.10
WS 0.03
YJ 0.07
WA 0.04
TA 0.05
LB 0.12
OP 0.23
UB 0.17
TP 0.19
Autumn (n = 7)
CC 0.04
B 0.01
JL 0.12
WS 0.03
YJ 0.02
WA 0.05
TA 0.04
LB 0.11
OP 0.24
UB 0.18
TP 0.17
Post-calving (n = 12)
CC 0.06
B 0.01
JL 0.01
WS 0.06
YJ 0.08
WA 0.12
TA 0.09
LB 0.06
OP 0.16
UB 0.19
TP 0.17
Summer (n = 12)
CC 0.01
B 0.01
JL 0.03
WS 0.12
YJ 0.02
WA 0.12
TA 0.10
LB 0.06
OP 0.16
UB 0.20
TP 0.17
Autumn (n = 10)
CC 0.07
B 0.06
JL 0.04
WS 0.07
YJ 0.07
WA 0.11
TA 0.09
LB 0.05
OP 0.12
UB 0.17
TP 0.16
Post-calving (n = 13)
CC 0.00
B 0.08
JL 0.06
WS 0.04
YJ 0.04
WA 0.10
TA 0.12
LB 0.11
OP 0.20
UB 0.11
TP 0.16
Summer (n = 11)
CC 0.00
B 0.03
JL 0.01
WS 0.03
YJ 0.01
WA 0.13
TA 0.12
LB 0.06
OP 0.30
UB 0.13
TP 0.18
Autumn (n = 12)
CC 0.00
B 0.04
JL 0.11
WS 0.03
YJ 0.02
WA 0.09
TA 0.07
LB 0.12
OP 0.30
UB 0.09
TP 0.14

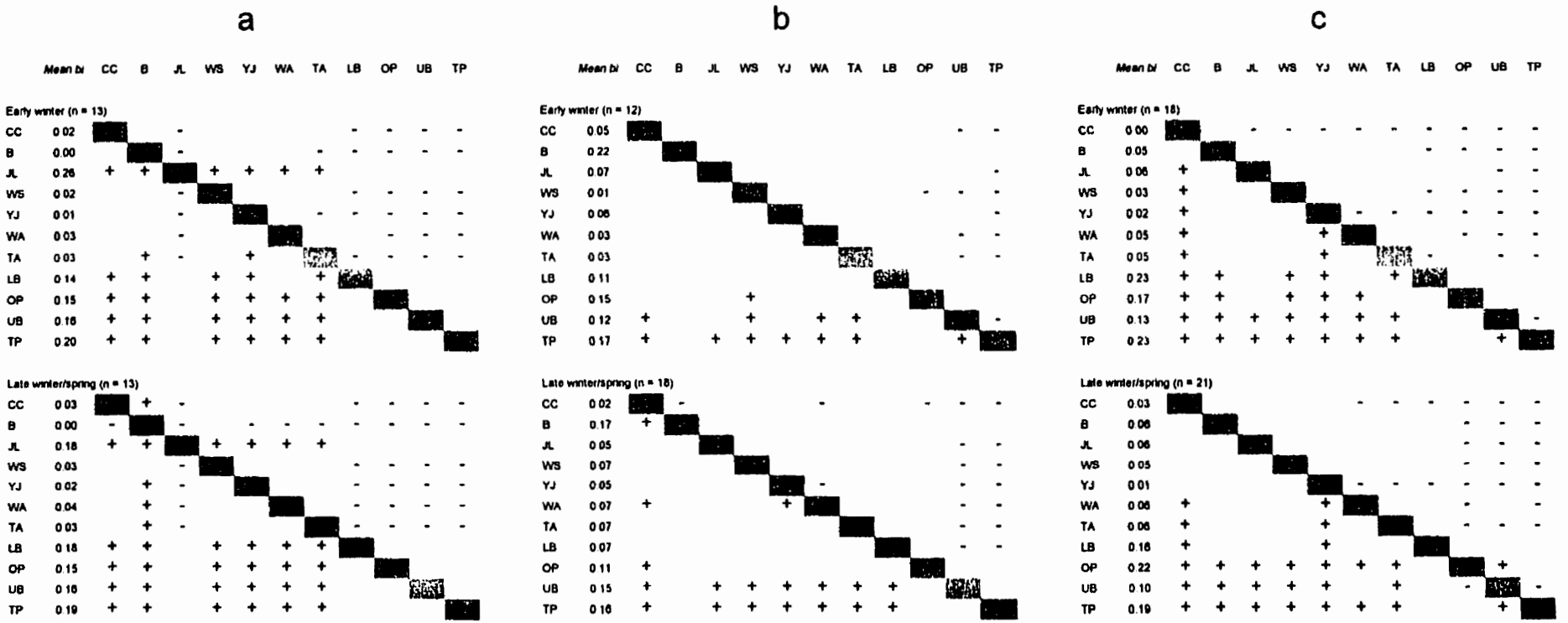


Fig. 4.4 Mean third order selection indices (b_i) and significant differences between ranks of pairs of the 11 habitat types in 5 seasons for three populations of woodland caribou in central Saskatchewan: (a) Weyakwin Lake; (b) Nemeiben Lake; and (c) Montreal Lake. Each row presents the mean selection index value for a habitat type and whether that type was selected significantly more (+) or less (-) than each habitat type listed in the columns. Codes for habitat types appear in Table 4.1.

n = the number of animal-seasons represented by the data.

forests and both open and treed peatlands. I observed little difference between post-calving and summer habitat selection other than an increase in the selection indices for open peatlands and a decline in the selection indices for clearcuts and burns during the summer. While habitat selection in autumn generally followed patterns observed in the summer, I observed less selective behaviour in autumn than during any other season (Fig. 4.4a-c).

Animals in the Weyakwin Lake population showed increasingly selective behaviour in the two winter seasons, continuing to choose peatland and black spruce/jack pine dominated forests but also increasing their selection of jack pine-lichen and lowland black spruce communities (Fig. 4.4a). Along with the treed peatland communities, the latter two habitat types have the highest abundances of both arboreal and terrestrial lichens. These five habitat types were selected almost to the exclusion of all other habitat types. The data from animals in the Nemeiben Lake population show that treed peatlands and black spruce/jack pine stands had the highest selection indices while clearcuts had the lowest selection indices (Fig. 4.4b). Individuals in the Montreal Lake population showed significant selection against clearcuts and young jack pine stands while preferring open and treed peatlands and black spruce/jack pine uplands throughout the winter. Montreal Lake animals preferentially used lowland spruce stands with

their abundant arboreal lichens in early winter (Fig. 4.4c).

4.4 Discussion

My results document highly selective behaviour by woodland caribou in central Saskatchewan. Selection was demonstrated at both spatial scales examined, and to a lesser extent, at both temporal scales. The habitats selected at the second order (coarser scale) were largely selected at the third order (finer scale) as well, though there were exceptions. I failed to detect a significant difference in habitat selection between reproductive classes, perhaps because 94% of my study animals were pregnant (Chapter 3). As a result, I expected virtually all the animals to have the same criteria in selecting calving locations and post-calving habitat. From the summer onward calves are as mobile as adults, and the factors affecting the behaviour of cows with and without calves may be the same, as reflected by the habitat selection patterns that I observed.

4.4.1 Second order selection

The patterns observed largely conform to the expected behaviour of woodland caribou if they were selecting habitats to avoid wolf predation. However, I did notice some exceptions to this trend. The Weyakwin Lake

population was in a region that was being actively logged during the study, and the Clarke Lake population inhabited an area that had been subjected to extensive logging activity in the decade prior to the study. Animals in both populations inhabited seasonal ranges that showed selective inclusion of clearcuts over some other habitat types. The Mossy River population was in an area whose uplands were burned extensively in the 1980s and early 1990s. The seasonal ranges of Mossy River caribou showed more selection favouring early seral stage jack pine stands than was found in the other populations. Relative selection of disturbed areas by each of these three populations may have been due to constraints on emigration, or due to the fact that there had yet to be sufficient time following disturbance to allow for moose populations to increase.

In Chapter 3 I described the caribou in the region as belonging to several populations within a metapopulation. I speculated that disturbances since the 1960s had fragmented what had likely been a continuous, though heterogeneous, distribution of woodland caribou in the region. The remaining populations may be relics, largely constrained by ecological barriers created by human activity in the region, and their second order habitat selection may better represent past habitat value than present selection.

The habitat types contained in the seasonal ranges selected by Clarke Lake animals differed among years of study. The data from 1995 show a decline in the mean selection index and relative preference for clearcuts over other habitat types when compared with data from the two previous years. This habitat change may have been stimulated by increased predation risk. Data for the Clarke Lake population showed a trend of lower adult female survival in 1994 than in 1993 or 1995 (Chapter 3).

4.4.2 Third order selection

While I did not suggest that woodland caribou in Saskatchewan were limited by factors other than predation (Chapter 3), it follows that at some scale the animals must select adequate forage. Consequently, I expected that at finer spatial and temporal scales I would observe selective behaviour become more responsive to limiting factors other than predation. The patterns of third order selection that I observed (Fig. 4.2b) were largely the same as those observed for second order selection. The differences between second and third order selection support the argument that the patterns inconsistent with predator avoidance at the second order may be artefacts of pre-logging distributions. The fact that Clarke Lake and Weyakwin Lake animals preferred clearcuts at the second order but avoided them (Fig. 4.2b) at the third order

suggests that it is sub-optimal habitat. It may be that in the first decade following logging, clearcuts do not represent moose habitat as they do when they become early seral stage forests (as might fall within the young jack pine and trembling aspen communities). Similarly, caribou at Mossy River decreased their selective use of young jack pine stands at the third order. Caribou in the Nemeiben Lake population also showed marked change in selection between the second and third orders, most notably with a large decline in their selection of water bodies.

The seasonal selection patterns that I observed suggest that female woodland caribou selected both black spruce dominated stands and peatlands throughout the year. The selection of peatlands and spruce uplands for calving and post-calving that I observed was also reported for forest reindeer (*R. t. fennicus*) in Finland, which calve in old spruce dominated forests with areas of spruce bogs near streams and peatlands (Helle 1980). Helle (1980) described the habitat selected in his study as a mosaic of the different habitat types, a pattern that was also observed in my study area during post-calving aerial surveys and by Thomas and Armbruster (1996). While caribou may select calving sites to avoid predation (Bergerud *et al.* 1984; Bergerud and Page 1987; Bergerud and Ballard 1988; Bergerud *et al.* 1990), they may be satisfying their dietary needs at the same time. The use of habitat mosaics may represent

selection both to accomplish reduced predation risk and optimal foraging (Helle 1980; Paré and Huot 1985). The spring diet of caribou in my study area was horsetails (*Equisetum* spp.), graminoids, and buckbean (*Menyanthyes trifoliata*) (Thomas and Armbruster 1996). These types of forage are associated with peatlands and are the same as the diet of woodland caribou inhabiting small (<100 ha) string fens in Québec (Paré and Huot 1985).

I observed that summer habitat selection was similar to post-calving selection, a pattern also reported by Helle (1980) who believed that the vegetation in spruce forest-peatland mosaics provided important nutrients for lactation. The highly selective behaviour exhibited in winter maintained separation from habitat preferred by moose and placed caribou in habitats containing abundant terrestrial and arboreal lichens as well as protein rich sedges and horsetails. Caribou winter diets are known to contain large amounts of all these items when available, both in areas with low predator densities (Miller 1976) and in my study area (Thomas and Armbruster 1996) where predation was the primary limiting factor.

4.4.3 Selection scale and limiting factors

Wiens (1989) cautioned that conclusions drawn at one scale may not apply at other scales. I agree with Levin (1992) who stated that all scales are not equally

important, and I further argue that the scale itself is a critical component of the conclusion. Quite simply, decisions made at coarser spatial and temporal scales should reveal more important environmental features than decisions made at finer scales. The hierarchy is not only one of space and time but one of relevance. Evolutionary relevance is judged by the ability of various factors to limit a population through natural selection acting on the individuals within the population. The ability to avoid the factors that are most limiting at each scale will maximize an individual's fitness. At different scales, the ability of different factors to affect individual fitness will vary. The critical thresholds of With and Crist (1995) should represent the points on the continuum at which the relative abilities of different factors to limit individual fitness are reversed. A domain of scale (Wiens 1989) should represent the range of scales over which individuals are responding to a specific (set of) limiting factor(s). A knowledge of factors limiting, or potentially limiting, a population can direct the scale of investigation to determine the environmental features that affect individual ability to overcome those limiting factors.

I suggest that all caribou have the same limiting factors and that they respond to them in the same order of priority: showing the strongest selection at the coarsest

scale for habitat that permits them to avoid the effects of the factor most able to limit their individual fitness. Like other migratory ungulates (Fryxell *et al.* 1988), barren ground caribou have been successful at avoiding predators through second order selection, and consequently can focus their finer scale selective activities on forage availability. Food has been shown to be the limiting factor for migratory caribou populations, and for caribou populations in areas where predators are absent (Messier *et al.* 1988; Adamczewski *et al.* 1988; Bergerud *et al.* 1990; Crête *et al.* 1990).

In Québec, woodland caribou that share their population range with white-tailed deer infected with meningeal worm select their home ranges (second order selection) such that they minimize contact with both deer and the coyotes that prey on them (Ouellet *et al.* 1996). Almost all woodland caribou populations have been unsuccessful in avoiding predators through first order selection. Because predation is the most important limiting factor for woodland caribou, they should avoid predation at the coarsest level of selection possible, in this case at the second order. If their attempts to avoid predators at this level do not meet with success, they must continue to select habitat to minimize predation at each finer scale of selection.

That predator-free habitats should also represent habitats in which caribou can meet their other needs is intuitive. In focusing on reducing predation risk, caribou may inhabit less productive habitat, reducing their foraging efficiency and increasing food competition (Ouellet *et al.* 1996). Coincident with their evolution as predator avoiders, caribou have evolved the ability to consume the forage in areas with low predator densities, *i.e.* lichens, a resource largely unexploited by other ungulates. While caribou thrive on other forages, and require them in their diets, they alone amongst the ungulates employ lichens as a dietary staple.

My findings are in keeping with those of Bergerud *et al.* (1990) who suggested that caribou reduce predation risk at a coarse grain and select forage at a fine grain. More generally, I suggest that the hierarchy of habitat selection should reflect the hierarchy of factors limiting an individual's fitness.

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5. General Discussion

The ability of habitat selection studies to reveal ecologically relevant and interpretable behaviour is dependent on finding answers to a suite of questions. The scales of investigation, the environmental features best employed in the delineation of habitat categories, and the identification of factors potentially limiting to a population are all critical to the study and explanation of selective behaviour. The relatedness of these attributes means that the process of studying habitat selection is iterative. The results of selection studies can divulge the scales at which individuals respond, can identify important environmental features, and can direct investigations into limiting factors. Similarly, a knowledge of limiting factors should direct habitat descriptions and study scales, while a knowledge of scales of response can lead to hypotheses regarding limiting factors and to the definition of relevant habitat categories. Information regarding any of these features should affect the investigation of the others.

I began my research by adopting the assumption that woodland caribou (*Rangifer tarandus caribou*) in

Saskatchewan would be like caribou elsewhere and limited likely by predation (*e.g.*, Bergerud 1983; Bergerud and Elliot 1986; Bergerud and Ballard 1988), though possibly by food (*e.g.*, Messier *et al.* 1988; Adamczewski *et al.* 1988; Bergerud *et al.* 1990; Crête *et al.* 1990). If woodland caribou in Saskatchewan are limited by food then variables representing caribou forage become critical; if they are limited by predation then variables representing forage for other ungulate species are critical (as predation is linked to the densities of other ungulate populations, Chapter 3). I considered food, predation, and other potentially limiting factors when determining which vegetation attributes to measure (Chapter 2).

The vegetation communities that I identified (Chapter 2) were highly correlated with overstorey characteristics. Carleton and Maycock (1981) explained this relationship as a fundamental characteristic of forest plant communities whose origin lies in the functional dependence between canopy and understorey vegetation. The practical consequence of this relationship is that the provincial forest inventory provides adequate information to infer the vegetation community types described in Chapter 2. Canonical correspondence analysis proved to be an important tool for assessing the degree of correspondence between data describing the entire vegetation communities and forest inventory data.

From an animal perspective, the quality of a given habitat type relates to its ability to affect an individual's lifetime reproductive success. From a research perspective, the objective of studying habitat selection by animals is to identify behavioural patterns and to then establish the relationship of selective behaviour with reproductive performance (Van Horne 1983; Hobbs and Hanley 1988). At the level of an individual population, the processes of interest become the rates of pregnancy, natality, mortality, and population growth. The study of these parameters requires prior identification of the population being studied.

In Chapter 3, I first identified the caribou populations and metapopulation being studied, then continued with an assessment of their demographic parameters. I interpreted the demographic data to be evidence that the caribou populations in the region were likely declining. I took the results on mortality and the high pregnancy and birth rates as evidence that the populations were limited not by food, but by predation, as expected (Chapter 3). As a result, I expected female woodland caribou to select habitat primarily for its predator-free qualities. These qualities are related to the vegetation communities described in Chapter 2.

Finally, in Chapter 4, I related habitat selection patterns to the vegetation communities described in Chapter

2 and explained them according to the limiting factors identified in Chapter 3. Unlike foraging decisions which might best be investigated near the scale of ingestion (Schaefer and Messier 1995), predator avoidance should relate to coarser temporal and spatial scales. The habitat selection component of my work was conducted both at a coarse (seasonal use) scale, and at a finer (daily use) scale. At the finer scale, I examined an area around each location in an attempt to represent habitat use as a composition of habitat categories, and to overcome telemetry bias.

I found habitat selection by female woodland caribou to be largely consistent at the two spatial scales examined (Chapter 4). Study animals preferentially selected peatlands and black spruce (*Picea mariana*) dominated stands relative to clearcuts, burns, and young jack pine (*Pinus banksiana*) dominated stands. The patterns of selection observed were consistent with the avoidance of habitat likely to contain higher densities of moose (*Alces alces*) which support higher densities of wolves (*Canis lupus*). Inconsistencies in this general pattern at the coarser scale were resolved at the finer scale. The changes in selection patterns from coarse to fine scale selection suggest that caribou avoid wolves at finer scales when they have not successfully avoided them at a coarser scale. Human disturbance is implicated as the ultimate cause of

caribou population decline due to the post-logging increase in habitat associated with higher moose and wolf densities (*e.g.*, Bergerud 1974; Forbes and Theberge 1993; Heikkilä and Härkönen 1996; Rempel *et al.* 1997).

Weins (1989) stated that the study of selection should occur at more than one scale, and that investigation at inappropriate scales may result in failing to detect real patterns. He further cautioned that when the scale is wrong, we may devise explanations to fit the observations when we may not have observed the system correctly (Wiens 1989). I argue that the patterns detected should be explained with reference to the factors potentially limiting the population. The significance and interpretability of the selection patterns presented in Chapter 4 are evidence that the habitat categories that I defined were also perceived by the animals. The identification of significant patterns of selection is related to simultaneously identifying the factors limiting the population, the environmental features best able to categorize habitat, and the appropriate scales of study. Furthermore, selective behaviour at coarser scales should relate to factors with a greater potential to limit lifetime reproductive success relative to finer scale selection. The ability to link the hierarchy of habitat selection to population dynamics requires only that animal behaviour be explained in the light of its effect on

reproductive success, in other words, with reference to natural selection.

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APPENDIX A: WINTER VEGETATION COMMUNITY CHARACTERISTICS

Table A.1 Mean vegetation characteristics of the six winter plant communities determined by cluster analysis. Units of measure are described below the table.

Taxon	Community					
	A	B	C	D	E	F
Trees*						
Abies balsamea		319		27		
Betula papyrifera		22	253	173	17	20
Larix laricina		90			172	17
Picea glauca		263		88		3
Picea mariana		473	113	48	1522	2893
Pinus banksiana	750	103	7253	42	856	835
Populus balsamifera		16		144		
Populus tremuloides		184	560	1450	56	42
Salix spp.			13	71		17
Shrubs†						
Abies balsamea		9.2		0.6		
Picea glauca		1.0	0.4	2.5		
Picea mariana		3.7	13.6	1.3	6.7	10.0
Pinus banksiana	1.1	0.2	4.2			
Herbaceous / Dwarf shrub†						
Abies balsamea		1.2		0.3		
Arctostaphylos uva-ursi	7.6	0.5	2.1		0.3	1.5
Aster spp.		0.1		1.0		
Chamaedaphne calyculata		0.4			4.4	
Cornus canadensis	0.9	3.3	1.2	6.5	0.8	0.8
Cyperaceae		0.3			3.5	0.3
Equisetum arvense		1.0		0.6		0.6
Equisetum pratense		0.4		0.3		
Equisetum sylvaticum			1.1	0.2		1.3
Lathyrus ochroleucus		0.3		2.6		
Ledum groenlandicum	2.2	7.6	8.7	1.9	11.3	12.5

Table A.1 continued

Taxon	Community					
	A	B	C	D	E	F
Linnaea borealis	1.3	2.4	1.0	4.8	0.4	1.2
Lycopodium annotinum		1.4		3.7		0.6
Lycopodium complanatum	0.9	0.3		0.2		0.2
Mitella nuda		1.6		0.5		
Picea mariana	0.3	0.5	3.2		0.3	1.0
Poaceae	0.8	1.6	2.8	14.2	2.2	0.9
Rubus chamaemorus		0.6			1.0	0.2
Vaccinium vitis-idaea	9.5	3.6	1.9	1.0	3.5	3.9
Vicia americana				0.9		
Mosses and lichens†						
Cladina mitis	50.4	2.0	0.4		13.2	2.8
Cladina rangiferina	0.7	0.1			1.8	1.6
Cladonia spp.	2.7	0.4	2.9		1.5	0.3
Dicranum spp.	2.6	1.1	3.2	0.4	0.7	1.7
Hylocomium splendens		11.7		0.7	6.5	10.5
Peltigera spp.	2.6	1.1	2.4		0.4	0.7
Pleurozium schreberi	10.1	16.5	1.9	1.4	23.2	54.3
Polytrichum spp.			13.0	0.1	1.2	0.6
Ptilium crista-castrensis		2.8			1.7	4.0
Sphagnum spp.		1.6	1.5		22.3	1.8
Non-vegetative cover†						
Litter	58.9	72.8	77.1	94.7	37.3	49.1
Arboreal lichen‡						
Total	15	14			97	24

* Tree cover expressed in stems·ha^{-1}.

† Shrub, herbaceous, dwarf shrub, moss, lichen, and non-vegetative cover expressed in percent cover. Values <0.1% are not shown.

‡ Arboreal lichen totals expressed in kg·ha^{-1}.

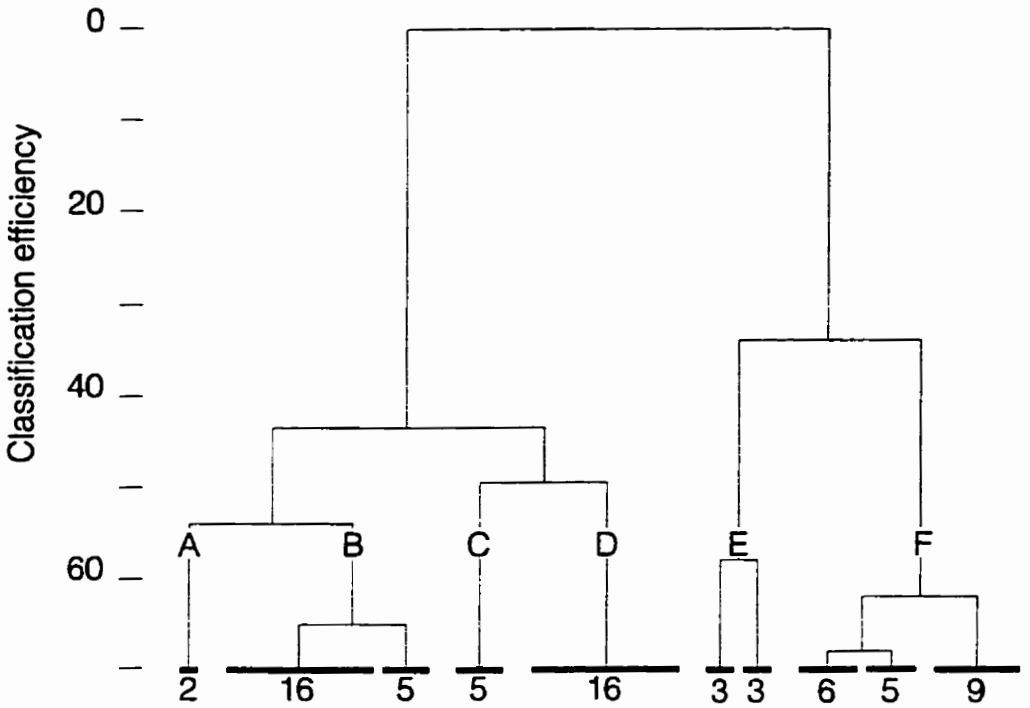


Fig. A.1 Sum of squares classification dendrogram of the 70 stands based on winter data. The six community types described in the text are indicated by the letters A-F. Numbers along the bottom of the figure indicate the number of stands contained in the corresponding branches.

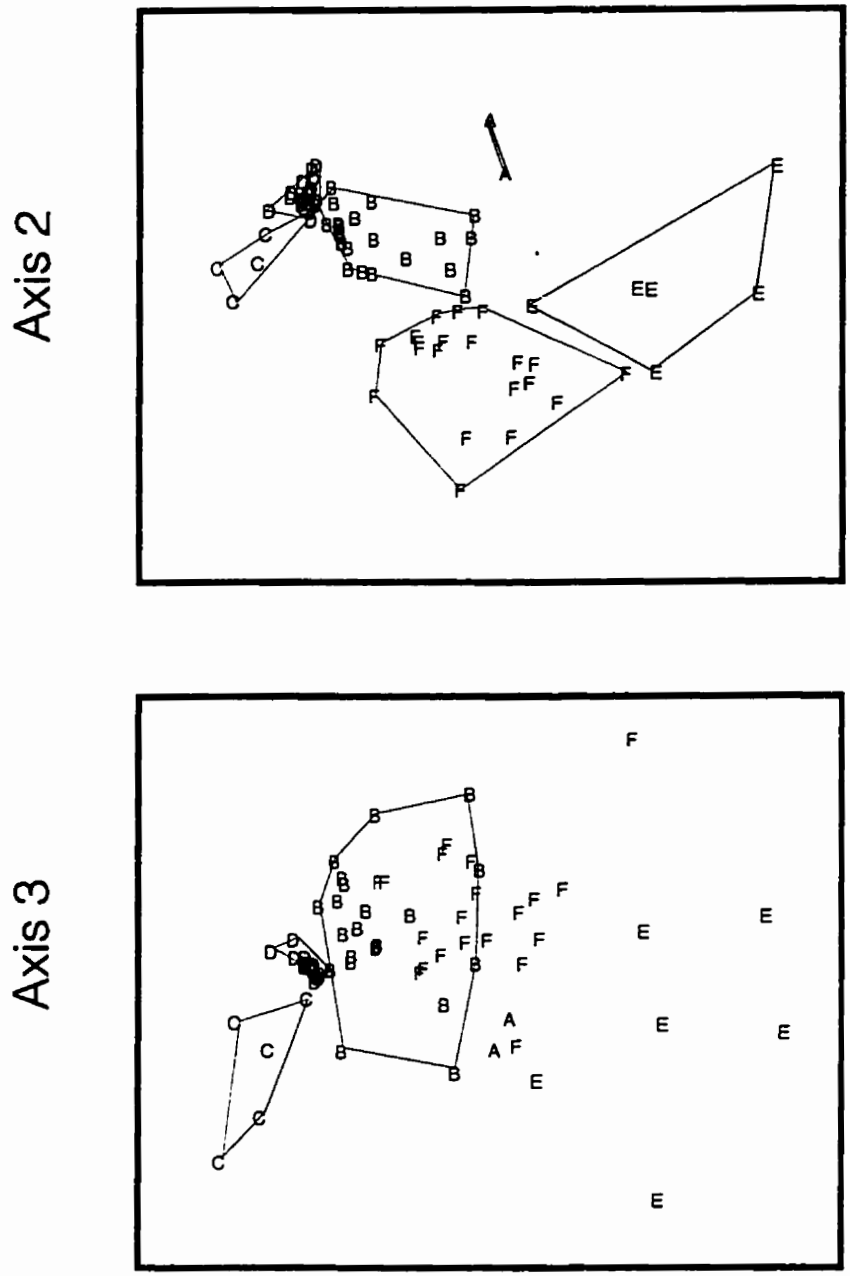


Fig. A.2 Nonmetric multidimensional scaling ordination of the 70 stands based on winter data. The letters A-F represent community membership identified by classification (Fig. A.1) and described in the text.

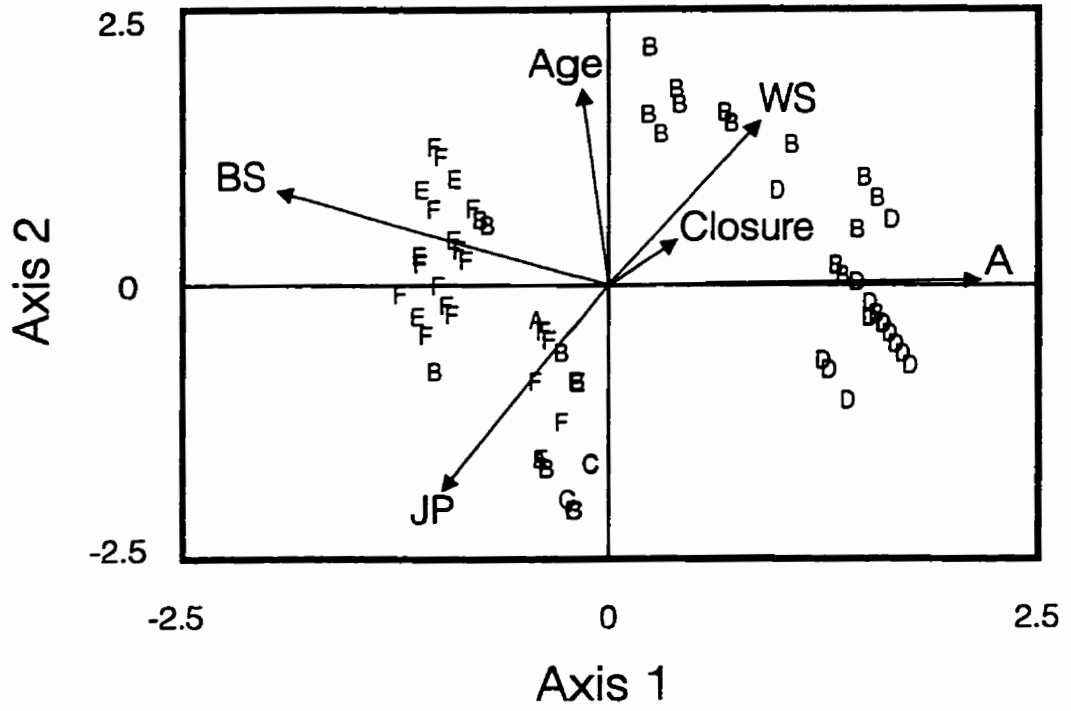
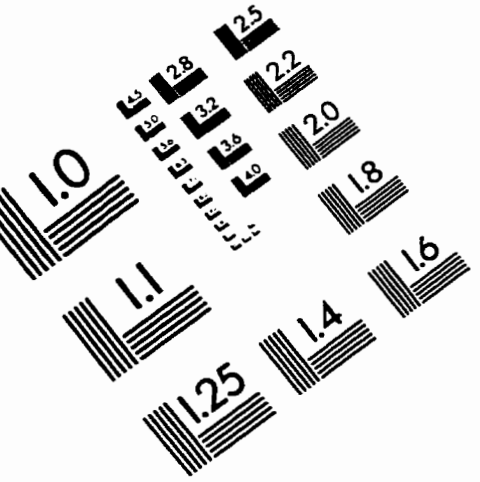
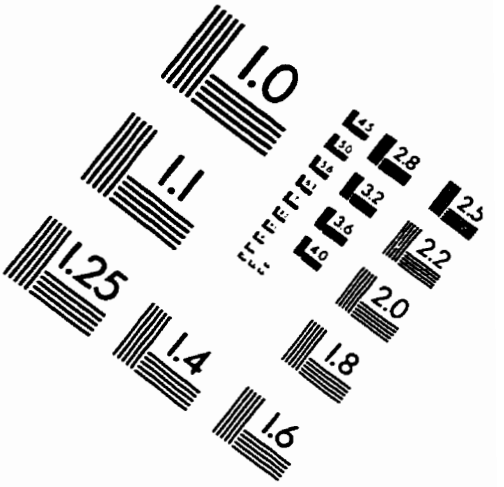
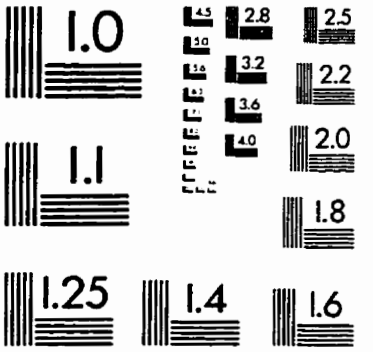


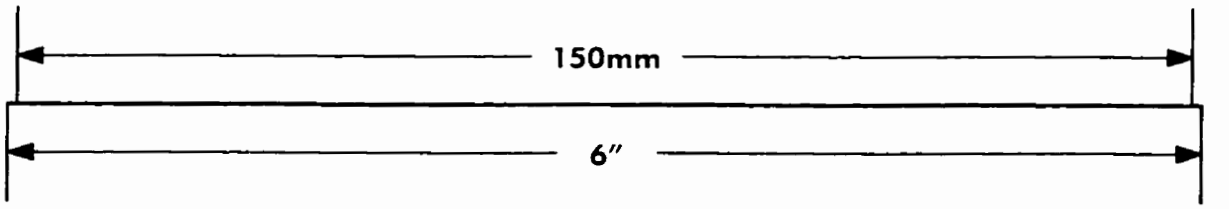
Fig. A.3 Biplot of canopy characteristics and stand types on the first two canonical correspondence analysis axes for winter data. The letters A-F represent community membership identified by classification (Fig. A.1) and described in the text. Canopy vectors are for age, closure, White spruce (WS), black spruce (BS), jack pine (JP), and aspen (A). Vector lengths shown are 2.5 x original values.

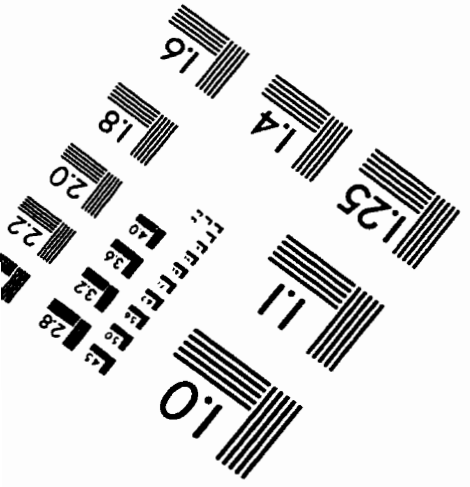
IMAGE EVALUATION
TEST TARGET (QA-3)

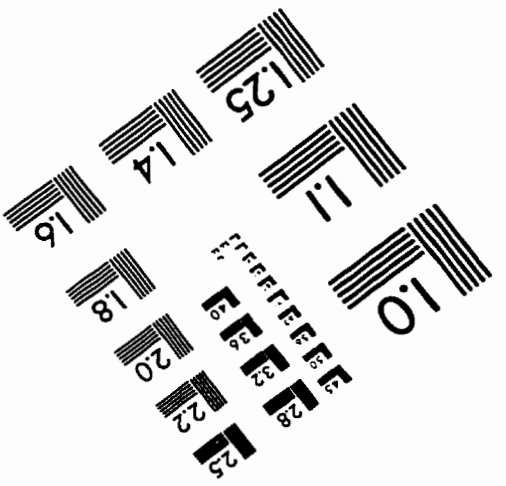












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